PATTERNS OF PRIMARY MOULT IN THE WEAVERS, PLOCEIDAE

Hans-Dieter Oschadleus

Thesis Presented for the Degree of

DOCTOR OF PHILOSOPHY

In the Department of Statistical Sciences
UNIVERSITY OF CAPE TOWN

September 2005

Supervisor: Professor L.G. Underhill
Avian Demography Unit
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Abstract

Patterns of renewal of feathers are poorly known in African birds. Moult is energetically costly and is thus an important part of a bird's annual cycle; moult needs to be fitted in with breeding activities, and in some species, migration. Ringers in southern Africa have been submitting primary moult data to SAFRING, the South African Bird Ringing Unit, since 1998, providing a large amount of data that the author has been curating and checking on an on-going basis as Ringing Coordinator. My main interest is in the weaverbirds and I have ringed several thousand Southern Masked Weavers *Ploceus velatus* and many other species. Les Underhill and Walter Zucchini developed a statistical model to analyse timing and duration of primary moult in a standardized way in 1988. Primary moult was analysed in the southern African weaverbird family using the Underhill-Zucchini method throughout. In some species, this method was applied to individual feathers as well as the whole wing.

Two weaver species are restricted to arid and semi-arid regions of southern Africa, the Sociable Weaver *Philetairus socius* and Chestnut Weaver *Ploceus rubiginosus*. Primary moult and biometrics were analysed in these species. Both species have a relatively slow moult as an adaptation to life in semi-arid regions. The Red-billed Quelea *Quelea quelea* is a migrant found throughout southern Africa, allowing comparisons of moult parameters in arid and mesic environments. Geographic variation in breeding seasonality and primary moult parameters was investigated in the following weavers in South Africa: Cape Weaver *P. capensis*, Southern Masked Weaver, Village Weaver *P. cucullatus*, Yellow Weaver *P. subaureus*, Spectacled Weaver *P. ocularis*, Thick-billed Weaver *Amblyospiza albifrons*, Southern Red Bishop *Euplectes orix,* Long-tailed Widow *E. progne*, White-winged Widow *E. albonotatus*, Red-collared Widow *E. ardens*, and Fan-tailed Widow *E. axillaries* and Yellow Bishop *E. capensis*.

Breeding and primary moult start earlier the Western Cape, a winter rainfall region, than in the summer rainfall region of South Africa. Two species, the Southern Masked Weaver and Thick-billed Weaver, have undergone range expansions in the last century and the new populations show evolving patterns in the timing of moult.

Annual variation in start date of moult was investigated in Cape Weavers, Southern Red Bishops and Southern Masked Weavers in the Western Cape. For the first

two species, there was wide variation in start dates due to variability in timing of rainfall in different years.

Primary moult followed closely after breeding. The annual cycle of southern African weavers was less variable in the mesic eastern part of southern Africa. The more regular rainfall of the mesic regions allowed weavers to grow more than one primary simultaneously. In the arid regions weavers grew one primary at a time.

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I would like to thank the ringers in southern Africa who have been enthusiastically submitting ringing data year after year and hoping that their data will be of some use somehow. It has been of incredible use! The ringers who have made the biggest contributions of data for each chapter are listed in the relevant chapter. I also appreciate the many helpers I have had myself over many years of ringing weavers in different parts of southern Africa.

Weaver wings for determining relative primary feather masses were provided by Corné Anderson (Sociable Weaver), Tim Osborne (Chestnut Weaver), Kevin McKann (Long-tailed Widow), and David Allan (Thick-billed Weaver). Rainfall data was provided by the South African Weather Service (chapters on Sociable Weaver, annual variation in moult), and by Tim Osborne (chapter on Chestnut Weaver).

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Chapter 1

Introduction

Introduction

The Introduction covers four aspects. Firstly, it sets the background of the family Ploceidae, a large family found in Africa and southern Asia. Secondly, it briefly describes the biogeography and breeding seasonality of the weavers in southern Africa. Thirdly, it provides an introduction to moult and explains the methodology of the statistical analysis for duration and start of primary moult. Lastly, it presents an outline of the thesis chapters.

A. Ploceidae

Lack (1968) considered weaverbirds such a particularly interesting family from the perspective of studying ecological adaptation that he devoted a full chapter of this influential book to them. In spite of this emphasis, many aspects of their life histories remain poorly studied nearly four decades later.

The weaverbirds are in a large family of birds found mostly in Africa, with a few species found in southern Asia and the West Indian Ocean islands (Craig 2004). Following Craig (2004), there are 116 species in 16 genera. These can be placed in three subfamilies which, in broad terms, consist of genera which make stick nests, grass nests and woven nests (Table 1). *Ploceus* is the largest bird genus in Africa (Benson *et al.* 1971). The weaverbird family is a diverse group, illustrated by the following extremes. The pest Red-billed Quelea *Quelea quelea* is considered by some to be the most numerous land-bird in the world, there being an estimated 1 500 million individuals (Elliott 1989). Contrast this with the rarest weaver: the threatened Mauritius Fody *Foudia rubra* with an estimated population of 210–250 birds (BirdLife International 2004). For such a large family the size range is relatively small; the smallest weaver is the Yellow-crowned Bishop *Euplectes afer* (mean wing of West African males 57.5 mm, Fry and Keith 2004) while the largest is the Long-tailed Widow *Euplectes progne* (mean wing of males 138 mm, Fry and Keith 2004). The communal nest of the Sociable Weaver *Philetairus socius* is the largest single structure built by any bird species in the world; it can weigh up to a ton and attain a width of 7 m and a height of 4 m (Tarboton 2001).

The weavers are largely seed-eating birds, in which they resemble sparrows Passeridae, buntings Emberizidae, canaries Fringillidae and waxbills Estrildidae in morphology; but some weaver species are mainly insectivorous (Moreau 1960). The bill is always straight, but varies from slender and sharp-pointed in insectivorous species to thick and conical in specialist granivores (Craig 2004). Granivores husk seeds, and large-billed species can crack seeds such as sunflowers and the kernels of forest fruits. All species seem to take insects opportunistically, and some are virtually omnivorous, and besides grain, include berries, nectar, flowers, arthropods and a few small vertebrates in their diet.

Sexes may be similar, or strongly dissimilar in plumage and size. Where similar, there is no seasonal change in plumage, but in highly dimorphic species males alternate between breeding and non-breeding plumages, the latter resembling that of the female (Moreau 1960). In most dimorphic species the male apparently does not moult into breeding plumage until at least two years old (Craig 2004), e.g. Southern Masked Weaver *Ploceus velatus* (Tarboton 1965). The breeding plumages are mainly red, black and yellow (carotenoids and melanins). The chemical precursors of carotenoids are acquired from the diet and cannot be synthesized by the birds *(Euplectes:* Kritzler 1943). In breeding plumage, the males of some *Euplectes* species have long ornamental tail feathers (Craig and Villet 1998). In some species there is a coloured patch in the flight feathers, or a distinctive epaulet on the wrist joint. There is no coloured pattern on the tail. There is often a seasonal change in bill colour in males. Female and non-breeding male plumage is generally a streaked, brownish 'sparrowy' pattern. Iris colour is often yellow or red or brown, sometimes differing according to sex or age class (Craig 2004).

The wings are short and rounded to long and pointed with 10 primaries (Maclean 1993). The 10th primary is 10–40% of the length of the longest primary (Moreau 1960). The flight of weavers is straight and direct, though many smaller species are highly manoeuvrable. The tail has 12 feathers in all weaver species. The outermost pair are generally the longest; this is also true of the species which have ornamental tail plumes in breeding plumage. On the ground, birds hop or walk while arboreal species are agile and are able hang upside down while probing bark and leaves.

There is a clear link between the feeding ecology and social organization of weavers, ranging from solitary, monogamous insectivores to colonial, polygynous granivores (Crook 1964). Crook (1964) described three main types of pair formation in the Ploceinae. Each of these three types is largely associated with a different habitat and a different type of breeding organization. In the first pair formation type, the male sings and chases the female, and builds a nest either during or after this period. This type occurs mainly in monogamous insectivorous species breeding solitarily in evergreen forest, and both parents help to feed the young. In the second type, the male builds a nest and then displays at it to attract a mate. This type is found mainly in polygynous graminivorous species breeding colonially in trees in savanna or acacia country. Each male defends an extremely small area in the colony, within which he first builds one nest to which he attracts a mate, and then builds another to attract a second mate, so that polygyny is successive. Each female raises her brood unaided. In the third type, the male builds a nest and then seeks to attract a female by aerial display and song-flight, and only after he has done so does he lead her to a nest. This type is found mainly in polygynous granivores breeding in tall annual grasses or reeds, each male defending a small territory within which, like the colonial species, he first builds a nest for one female, and after he has obtained a mate, builds another nest for a second mate, and so on. The nests are dispersed within the male's territory and each female raises her brood unaided.

In addition to the social organization of the Ploceinae, the following types of social organization are found in other weaver subfamilies: communal breeding in a single nest structure in one species, the Sociable Weaver; co-operative breeding in family groups in a few species; and a lek mating system is known for one grassland species, the Jackson's Widowbird *Euplectes jacksoni* (Andersson 1991).

Weaver nests represent one of the most remarkable constructions produced by any animal. In most species the male makes the major contribution to nest construction, and the female adds lining if she accepts a nest. In the 'true' weavers (subfamily Ploceinae) males construct intricately woven nests using thin strips of plant material. Typically, nest-building starts with the construction of a bridge between supports, usually thin twigs. The male then perches on this bridge while weaving the nest bowl (Collias and Collias 1964). The nest entrance is either to the side or faces vertically downwards; in some species it is

extended into a tunnel from 10 cm to more than 1 m long. Nests of buffalo-weavers (Bubalornithinae) and sparrow-weavers (Plocepasserinae) are composed of dry pieces of vegetation, inserted and interlocked into a complex structure without any weaving or knotting (Collias and Collias 1964). Several weaver species strip the leaves of the twigs around their colonies; this makes the colony more visible but it may be a displacement activity (Oschadleus 2000). In the polygynous species, males build a succession of nests to which they attract females by displaying; the females line the nest, lay, incubate, and rear the nestlings with no or little male assistance. Colonies can consist of hundreds of males or single males (Tarboton 2001). In the monogamous species, sexes share parental duties and build a single nest per breeding season (Tarboton 2001).

Clutch size is 2–6, usually 2–3. The egg colour is varied, with the ground colour often bluish, plain, lightly spotted, or heavily patterned (Schönwetter and Meise 1983). In some species the egg colour is fixed while in others there is enormous individual variation in the ground colour and markings of eggs produced by different females. As many as 10 egg groups have been identified for Southern Masked Weavers (Hunter 1961). This may be an evolutionary response to parasitism by cuckoos or to intraspecific nest parasitism *(Ploceus:* Freeman 1988). The Diederik Cuckoo *Chrysococcyx caprius* is a brood parasite of weavers, in particular Baglafecht Weaver *Ploceus baglafecht*, Cape Weaver *P. capensis*, Golden Weaver *P. xanthops*, Lesser Masked Weaver *P. intermedius*, Southern Masked Weaver, Village Weaver *P. cucullatus*, Spectacled Weaver *P. ocularis* (Freeman 1988); also Bocage's Weaver *P. temporalis*, Black-winged Bishop *Euplectes hordeaceus*, Southern Red Bishop *E. orix* and Red-headed Weaver *Anaplectes rubriceps* (Colebrook-Robjent 1984).

Nestlings are naked with small patches of down on the feather tracts. The inside of the mouth is red and there are no mouth markings (Craig 2004). In all the Ploceidae the nestlings are altricial (Tarboton 2001).

The taxonomy of the Ploceidae has been revised several times over the last 100 years, the main revisions being by Chapin (1917) and Moreau (1960). In the past the sparrows have frequently been included as a sub-family of the weavers, but recent authorities have separated the sparrows from the weavers because of the distinct electrophoretic patterns of egg-white proteins (Sibley 1970). Sibley and Monroe (1990),

using a major higher-level re-organization on the basis of DNA-hybridization studies, placed the Ploceinae as a sub-family of the Passeridae (subfamily Ploceinae). Craig (2004), however, retained Ploceidae as a family and this arrangement is followed here. The genus *Ploceus* has 63 species and the whole family is in need of a new phylogeny based on genetic studies.

In southern Africa there are 29 species in eight genera (Table 1): Red-billed Buffalo-weaver, White-browed Sparrow-weaver, Sociable Weaver, Scaly-feathered Finch, Thick-billed Weaver, 12 *Ploceus* species, three *Quelea* species, and nine *Euplectes* species (Maclean 1993). Distributions of these species have been mapped in detail (Harrison *et al.* 1997). Eggs of all, and nests of many, southern African species are illustrated in Tarboton (2001).

B. Biogeography and breeding of the southern African weavers

The annual cycles of birds are affected by the environments in which they live. Southern Africa is a large region, with an exceptional variety of climatic factors. Within southern Africa there are strong climatic gradients from east to west, with rainfall (Figure 1) being the key factor (Allan *et al.* 1997). This has an effect on bird distributions within the subregion (e.g. Harrison *et al.* 1997), as well as an effect on life-history parameters (Lepage and Lloyd 2004).

In southern Africa there are three main regions with different rainfall patterns: the winter rainfall region of the Western Cape, with a typical Mediterranean climate, the south coast region with rain throughout the year, and the summer rainfall region over the remainder of South Africa (Allan *et al.* 1997, Figure 1). Within the summer rainfall region, especially along the latitudinal band between 24°S and 30°S, there is a striking rainfall gradient from the mesic subtropical coastal forest on the east coast to desert on the west coast. A more subtle variation is in the timing of the onset and peak of the summer rains; this is earliest in the southeastern section of the summer-rainfall region in KwaZulu-Natal and latest in the northwest, in northern Namibia (Figure 1). It is also noteworthy that the winter-rainfall region of the Western Cape lies on the same latitudinal band (32°–34°S) as the summer-rainfall region of the Eastern Cape; this makes

it possible to study the effect of seasonality of rainfall on the annual cycle of bird species (including the timing of moult) independent of the effect of day-length.

The western parts of southern Africa have a lower and less predictable rainfall than in the eastern parts. Lepage and Lloyd (2004) found clutch size in 106 bird species to be smaller in the more arid regions because this favours a bet-hedging strategy. Lepage and Lloyd (2004) suggested that birds in arid regions breed irrespective of rainfall, but increase clutch size when rain does fall, to maximize breeding success in an unpredictable environment.

There is a large variation in vegetation zones within southern Africa. The Western Cape largely contains the fynbos biome, while Gauteng and KwaZulu-Natal have mainly savanna and grassland biomes. The Eastern Cape has a mixture of biomes. Allan *et al.* (1997) provided a good introduction to the vegetation zones of southern Africa in relation to its avifauna.

The southern African weavers fall into three broad distributional groups (Table 1): five species in Arid and semi-arid west, dry woodland; 10 species found mainly in the mesic eastern parts of southern Africa, although their biogeographic preferences are broader in some species outside of this region; 10 species are found throughout the region or have intermediate distributions covering mesic and semi-arid habitats. The remaining four species have restricted ranges in Zimbabwe or Mozambique.

Breeding seasonality data were obtained from the BirdLife South Africa Nest Record Card Scheme (RP Prŷs-Jones and I Newton unpublished data). They estimated the month of laying of the first egg for each nest record and then summarised breeding seasonality for all birds in South Africa by presenting monthly totals of clutches laid per species per region. To compare breeding seasonality of weavers, the tabulated data of Prŷs-Jones and Newton were used to estimate the median and the 5th and 95th percentiles for each species and region in Chapters 5-7. Possible biases are that the Nest Record Cards may not cover the entire breeding season in all regions; the Nest Record Card records were not collected in the same years as the moult data; the sample size may be low for some species in some regions. The sample sizes for the species and regions with moult data, however, are large and collected randomly (by different observers in different years), giving confidence in the results obtained.

C. Moult and the analysis of moult

Feathers

Feathers are unique to birds. Feathers are used for flight, thermoregulation, camouflage and display. Flight and body feathers wear out and need to be regularly replaced in a predictable way and usually on an annual time-scale (Stresemann and Stresemann 1966). This is termed 'moult' and is necessary to ensure future survival because old feathers are constantly abraded due to behavioural activities, exposure to sunshine and other environmental stresses (Jenni and Winkler 1994). Small passerine birds moult all their flight feathers at least once a year (Jenni and Winkler 1994); there is a small number of passerines that moult twice a year (e.g. Willow Warbler *Phylloscopus trochilus*, Underhill *et al.* 1992; Black-chested Prinia *Prinia flavicans*, Herremans 1999); a list of seven species is given by Prŷs-Jones (1991). The most common pattern, found in adult breeders of most sedentary species in temperate and arctic regions as well as most migratory species, is that moult occurs soon after termination of breeding (post-nuptial moult); this is a moult of all body and all flight feathers. A proportion of migrants, especially long distance migrants, delay moult until after their southwards migration (Jenni and Winkler 1994). There is usually also a moult of the body feathers before breeding (pre-nuptial moult). Even among European passerines, living under relatively uniform environmental conditions, there are diverse strategies for the coping with the problem of fitting primary moult into the annual cycle (Jenni and Winkler 1994).

Moult and the annual cycle of birds

Moult is energetically demanding, both in terms of energy and nutrients (Murphy 1996) and time (Langston and Rohwer 1996). Thus timing of moult plays an important part in the annual cycle of a bird to reduce conflict with other energetically costly events, such as breeding and, in many species, migration (Murphy and King 1992). Thus moult in passerines usually follows soon after breeding (Payne 1972) so it can be completed before migration and/or the unfavourable conditions (e.g. less food supply) of mid winter.

The rate at which new feather mass is accrued is a physiologically and energetically important factor. Dawson *et al.* (2000) demonstrated that for some European passerine species total mass of new primary feathers increases at a constant rate throughout most of the duration of moult and hypothesized that this was a universal feature of moulting birds. The rate of increase in total mass is constant because the number of feathers being grown concurrently decreases as moult progresses toward the outer primaries (Dawson and Newton 2004). For if breeding is delayed, the start of moult is delayed resulting in more rapid moult of poorer quality, less massive feathers (Dawson *et al.* 2000). This is an adaptive mechanism mediated by decreasing day lengths that allows late-breeding birds to complete moult in time. Delaying breeding and moult in Blue Tits *Parus caeruleus* experimentally, resulted in higher thermoregulatory costs in the following winter and reduced survival and breeding success in the following season (Nilsson and Svensson 1996). Birds breeding late tend to start moult later than non-breeders and birds completing breeding early; late breeders then tend to moult more quickly (Morton and Morton 1990).

The annual cycle seems to rely on an endogenous rhythm organizing annual events like breeding, moult and migration (Gwinner 1996). This circannual clock is species- or population-specific and seems to be synchronized by environmental cues such as photoperiod. Moult strategies are not readily related to a few environmental factors in general (Salewski *et al.* 2004) and our understanding about these ecological factors is limited (see Jenni and Winkler 1994).

The quantitative description of primary moult

The key parameters of moult in a population are the average starting date and the duration. These parameters need to be studied in the context of the timing of the other major events in the annual cycle: breeding and, in some species, migration (Underhill 2003). For moult studies in many species, it is appropriate initially to focus on the moult of the primary wing feathers, because the main annual moult duration of many other feather tracts takes place within the period of moult of the primaries (Underhill 2003).

Collecting moult data in the field is most frequently undertaken by allocating individual primaries with a score from 0 to 5, where 0 = old feather, 1 = missing or

feather in pin, 2 = one-third grown, 3 = two-thirds grown, 4 = four-fifths grown, 5 = new feather (Ginn and Melville 1983). The primaries are numbered 1 (innermost) to 10 (outermost). In weavers, the 10th primary is reduced; sometimes it is still easily visible, e.g. Chestnut Weavers *Ploceus rubiginosus*, while in many *Euplectes* species it is minute. Traditionally, these individual feather scores are added to give the 'moult score' for a bird on a particular day, as proposed by Ashmole (1962) and developed by Newton (1966). For example, the string of digits 5542000000 indicates that the innermost two feathers are new, the third is four-fifths grown, the fifth is one-third grown, and the remainder are still old; the moult score is 16. For species with 10 primary feathers, moult score therefore increases to 50 when moult is complete. The standard scoring method is convenient for assessing the stage of moult. However, it has the weakness that equal weight is given to each primary feather although the actual lengths and masses of primary feathers may differ considerably. Because the outer primaries are generally larger than the inner ones, moult score does not increase linearly through time but exaggerates moult rate during the early part of moult and underestimates it later. This nonlinearity presents problems when moult-score data are used to estimate timing and duration of moult. Analyses of moult-score data using standard linear regression methods are inappropriate (Summers *et al.* 1983, Underhill and Zucchini 1988).

Prater (1981) noted that the lack of standardization of methods for the analysis of moult made it difficult to make comparisons between moult studies. There is a danger that apparent differences in duration of moult between species or across latitudes are statistical artifacts rather than genuine effects. Prater (1981) also noted the lack of satisfactory methods for estimating the parameters of moult, especially duration of moult. The development of rigorous methods to estimate the parameters of moult was undertaken by Underhill and Zucchini (1988) and Underhill *et al.* (1990). This method relies on a moult index that increases linearly in time; the best available approximation to this to date is to use 'percentage feather mass grown' as a moult index (e.g. Dawson *et al.* 2000), and this requires a knowledge of the masses of individual primary feathers (Summers *et al.* 1980).

To determine the masses of primary feathers, individual feathers from wings of weaver specimens were oven-dried at 60°C for 24 hours and then weighed on a balance

(Ohaus GA200D, precision 0.0001g) (compare Underhill and Summers 1993). Underhill and Joubert (1995) have shown that small samples are adequate to determine the relative masses of primary feathers for a species, because there is little intra-specific variation in this characteristic. The Underhill-Zucchini moult model developed by Underhill and Zucchini (1988) was applied to the data sets. Three types of moult data can be analysed:

1. birds classified only as not yet moulted, in moult and completed moult
2. as for type 1, but the moult indices are available for all birds in moult
3. only available data are the moult indices for the birds in moult

In this study all the data were considered to be of 'type 2' of the five types described by Underhill and Zucchini (1988) and Underhill *et al.* (1990), because full moult scores were recorded for each bird and all birds were considered available for sampling throughout the moult period. The parameters of primary moult were estimated using the moult index recommended by Summers (1976) and Summers *et al.* (1980, 1983), designed to reduce the bias introduced by the fact that the individual feathers are of different masses. The moult index used was percentage feather mass grown (PFMG), calculated according to the method of Underhill and Summers (1993). This transformation has been demonstrated to increase sufficiently linearly with time to reduce, and in some cases, to eliminate, bias in moult parameter estimation (Summers 1980; Summers *et al.* 1980, 1983). Because it is based on feather mass, the Underhill-Zucchini method with PFMG index is of greater physiological and energetic relevance than the standard method based on moult score.

An analysis of the moult of Willow Warblers *Phylloscopus trochilus* was the first to apply the statistically rigorous Underhill-Zucchini moult model to make comparisons on a large scale across various moult localities (Underhill *et al.* 1992). This has been followed up by Serra (1998) undertaking a similar study for Grey Plovers. A problem with the use of the Underhill-Zucchini method has been the lack of availability of the associated computer software. The programme developed by W. Zucchini needs skilled intervention to ensure that it converges to the correct result, and a user-friendly version has not yet been produced by the originators of the method (Underhill 2003). In spite of

this shortcoming, many analyses have been published using the Underhill-Zucchini model (Table 2).

Studies of primary moult using the Underhill-Zucchini method focused mainly on the primary feathers as a single unit. Serra (2002) investigated the parameters of moult of individual primary feathers of Grey Plovers *Pluvialis squatarola*. Serra's detailed analysis of the data for this species showed interesting differences between the strategies used by populations moulting under differing climatic conditions. A problem with this type of feather-by-feather analysis is a need for large sample sizes, preferably in excess of 1000 birds in moult. In addition, these samples need to be well spread throughout the moult period; otherwise it is not possible to make satisfactory estimates of the moult parameters for each primary. Because the feathers are being dealt with individually, there is no need to make the transformations recommended when the entire primary moult tract is analyzed (Summers 1980; Summers *et al.* 1980, 1983). Moult scores between 0 and 5 of individual feathers were converted to the values 0, 0.125, 0.375, 0.625, 0.875 and 1, respectively, to form a moult index lying between 0 and 1, as required by the Underhill-Zucchini model. Using the Underhill-Zucchini model to estimate the parameters of moult for individual primary feathers, has also been applied to selected species of waders (Underhill 2003).

Brandao (1998) (see also Underhill *et al.* in press) extended the Underhill-Zucchini (1988) moult model further to estimate starting dates for groups of birds (e.g. males and females, or annual groups), holding the other two parameters (duration and standard deviation) common to all groups. The motivation for this approach is that it is the starting dates that are likely to be the most variable; exceptionally large volumes of data are needed for each group to be able to estimate both starting dates and duration reliably (Brandao 1998). She also developed rigorous statistical testing procedures, using the likelihood ratio test, of the null hypothesis that the starting date for each group was the same. These extensions effectively enable analyses to be performed with a single "grouping" variable, analogous to one-way analysis of variance. This method was used to analyse inter-annual variation in moult in several species, differences between timing of moult of male and female Chestnut Weavers, and differences in moult parameters in two

different provinces of South Africa. Brandao's (1998) models also need the development of user-friendly versions.

Presentation in tables of the statistical results of the Underhill-Zucchini moult model includes the following information: mean starting date, standard deviation of the start date, mean duration of moult, and mean completion date. The Underhill-Zucchini moult model assumes that the distribution of starting dates has a normal distribution, which has two parameters: mean and standard deviation. The mean of this distribution is interpreted as the mean starting date of moult in the population and the standard deviation measures the extent of variability about the mean. If the standard deviation is small then moult is synchronized and vice versa. Thus 95% of birds are estimated to start moult during the period from 1.96 standard deviations below the mean to 1.96 standard deviations above the mean. The third parameter of the Underhill-Zucchini moult model is the duration of moult of the average bird. For each of the parameters, its standard error is also estimated. 95% confidence intervals for each parameter are given by the parameter estimate plus and minus 1.96 times the standard error of the parameter estimate. There were not enough recapture records within a moult season to estimate moult parameters from recaptures. The moult records are plotted as relative feather mass versus date for different individuals, including a small number of recaptured individuals.

Possible biases in the moult data are that some birds may move after breeding or before the end of moult; some individual birds may be less easily trapped than others (e.g. females versus males, or late breeders that start moult slightly later than the rest of the population). Other than Red-billed Quelea, weavers are not migrants, particularly in the areas studied. The possible bias of movements in the Red-billed Quelea is addressed in Chapter 4. Most weavers are trapped by ringers at dawn at roosting or breeding sites, and thus trap-shyness is not considered to have any great effect on the data. Birds with arrested moult were omitted from analyses – this involved relatively small numbers of birds, and arrested moult was recognized as adjacent old and new feathers with no growing feathers. If one primary had completed growth before the next fell out, there would still be a feather sheath requiring the feather to be scored as 4 rather than 5 (new); this would prevent confusing arrested moult with slow moult. Weavers were captured by ringers through the year, minimizing biases of early and late moulters having different

rates of moult; i.e. in this thesis the data presented includes all birds and presents population averages. Another potential source of error is in not analyzing secondary moult together with primary moult. Usually the secondary feathers start moulting when Primary 6 is moulted, thus the end of primary moult may be influenced by the energy needed to simultaneously start moult of the secondary feathers. For this thesis, secondary moult data were not available but are considered to have a similar effect on all species, reducing the error in the comparative studies presented here.

There is remarkably little available information relating to the primary moult of weavers from elsewhere in Africa (Table 3). With two exceptions, papers which allude to primary moult of weavers unfortunately present only the moult scores for a very small sample of captured birds or contain a vague comment about the timing and/or duration of moult.

D. A 'roadmap' of the thesis

Background and objectives

The data used in this thesis are from the SAFRING database, data being submitted by many ringers, including my own data. When I was appointed as SAFRING's bird ringing coordinator in 1998, I encouraged ringers to submit ringing data electronically instead of on paper schedules. I also encouraged ringers to submit mass, wing length and primary moult instead of just mass, in addition to the usual data (ring number, species, date, locality, etc). It has been encouraging to see ringers enthusiastically embrace the new changes, although it has taken a lot of work to train ringers in the recording of moult protocols, and for ringers to learn how to use computers, etc. From July 2004 onwards all ringing data have been computerized. Old ringing records are being computerized, although the paper schedules do not include moult data. This has provided a large database ready for analysis, for instance of historical changes of bird distribution, biometric analyses, and particularly of moult analyses. Moult is poorly studied in African birds (Craig 1983) and due to my interest in weaverbirds, I wanted to analyse moult of the weavers. These analyses will be fed back to the ringers to aid them in understanding

and appreciating birds in the hand even more. Thus this thesis is a tribute to the ringers of southern Africa.

Structure of thesis

In addition to this Introduction and the Conclusion, this thesis consists of seven chapters that have been prepared as papers for publication – Chapter 2 has been published (Oschadleus 2004), Chapter 3 is in press and Chapter 4 has been submitted for publication. The format used for each chapter is similar to that used by the journal of African ornithology, Ostrich.

Chapter 2 describes the biometrics and primary moult of the Sociable Weaver, a southern African endemic. Chapter 3 describes the biometrics and primary moult of another species inhabiting a semi-arid region, the Chestnut Weaver *Ploceus rubiginosus* in Namibia. Chapter 4 shows how primary moult duration and timing in Red-billed Quelea *Quelea quelea* varies in different parts of southern Africa so that completion of moult occurs at roughly the same time. Chapter 5 explores the geographic variation in breeding seasonality and primary moult parameters in Cape Weavers, Southern Masked Weavers and Southern Red Bishops in South Africa. Chapter 6 shows that breeding seasonality and primary moult parameters are similar in the *Euplectes* species in the summer rainfall region of South Africa. Chapter 7 describes breeding seasonality and primary moult parameters of Village Weaver *P. cucullatus*, Yellow Weaver *P. subaureus*, Spectacled Weaver *P. ocularis* and Thick-billed Weaver *Amblyospiza albifrons* in KwaZulu-Natal and also in Gauteng for the latter species. Chapter 8 investigates annual variation in start date of moult in Cape Weavers, Southern Red Bishops and Southern Masked Weavers in the Western Cape. Chapter 9 gives an overview of timing and seasonality of breeding and of primary moult in southern African weavers.

This is the first thesis to tackle both an intra- and inter-species study of patterns of primary moult using the Underhill-Zucchini method (Table 2). The only intra-species studies are those on the Willow Warbler (Underhill *et al.* 1992) and on the Grey Plover (Serra 2002). The only inter-species study is on a few wader species (Underhill 2003). The only published moult studies for weavers using the Underhill-Zucchini method are

for Southern Masked Weavers (Oschadleus *et al.* 2000) and five weaver species in the Eastern Cape (Craig *et al.* 2001).

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Table 1: Weaver genera of the world, and a list of the southern African weaver species
Mating system: M = monogamous, P = polygynous, c = co-operative breeder (from Tarboton 2001)
Region: A = arid and semi-arid west, dry woodland; M = mesic east; T = throughout or intermediate; R = restricted range
Moult studied: y = species included in this thesis, n = moult not studied in this thesis

Subfamily	Genus	No. of species	Southern African species	Mating system	Region	Moult studied
Bubalornithinae – buffalo weavers; stick nests						
	Bubalornis	2	Red-billed Buffalo-weaver *Bubalornis niger*	P	A	n
	Dinemellia	1				
Plocepasserinae – sparrow or social weavers; grass nests						
	Plocepasser	4	White-browed Sparrow-weaver *Plocepasser mahali*	M, c	A	n
	Histurgops	1				
	Sporopipes	2	Scaly-feathered Finch *Sporopipes squamifrons*	M	A	n
	Pseudonigrita	2				
	Philetairus	1	Sociable Weaver *Philetairus socius*	M, c	A	y
Ploceinae – true weavers; woven nests						
	Malimbus	10				
	Anaplectes	1	Red-headed Weaver *Anaplectes melanotis*	M or P	T	n
	Ploceus	63	Lesser Masked Weaver *Ploceus intermedius*	P	T	n
			Spectacled Weaver *Ploceus ocularis*	M	M	y
			Cape Weaver *Ploceus capensis*	P	T	y
			Yellow Weaver *Ploceus subaureus*	P	M	y
			Golden Weaver *Ploceus xanthops*	M or P	T	n
			Southern Brown-throated Weaver *Ploceus xanthopterus*	P	T	n
			Southern Masked Weaver *Ploceus velatus*	P	T	y
			Village Weaver *Ploceus cucullatus*	P	M	y
			Chestnut Weaver *Ploceus rubiginosus*	P	A	y
			Dark-backed Weaver *Ploceus bicolor*	M	M	n
			Olive-headed Weaver *Ploceus olivaceiceps*	(M)	R	n
	Pachypantes	1				

Table 1 continued

Subfamily	Genus	No. of species	Southern African species	Mating system	Region	Moult studied
	Amblyospiza	1	Thick-billed Weaver *Amblyospiza albifrons*	M or P	M	y
	Quelea	3	Cardinal Quelea *Quelea cardinalis* *	P	R	n
			Red-headed Quelea *Quelea erythrops*	M	M	n
			Red-billed Quelea *Quelea quelea*	M	T	y
	Brachycope	1				
	Euplectes	17	Yellow-crowned Bishop *Euplectes afer*	P	T	n
			Black-winged Bishop *Euplectes hordeaceus*	P	R	n
			Southern Red Bishop *Euplectes orix*	P	T	y
			Yellow Bishop *Euplectes capensis*	P	T	y
			Fan-tailed Widow *Euplectes axillaris*	P	M	y
			Yellow-mantled Widow *Euplectes macrourus*	P	R	n
			White-winged Widow *Euplectes albonotatus*	P	M	y
			Red-collared Widow *Euplectes ardens*	P	M	y
			Long-tailed Widow *Euplectes progne*	P	M	y
	Foudia	6				

* vagrant (1 confirmed record)

Table 2: Species with published studies using the maximum likelihood method of Underhill-Zucchini (1988) method to analyse primary moult

Species	Reference
Sooty Shearwater *Puffinus griseus*	Cooper *et al.* (1991)
Ruddy Turnstone *Arenaria interpres*	Summers *et al.* (1989), Underhill (2003)
Grey Plover *Pluvialis squatarola*	Serra (1998, 2002 and papers listed therein), Underhill (2003)
Sanderling *Calidris alba*	Underhill and Zucchini (1988), Underhill (2003)
Knot *Calidris canutus*	Underhill (2003)
Sanderling *Calidris alba*	Underhill (2003)
Redshank *Tringa totanus*	Underhill *et al.* (1990)
Bristle-thighed Curlew *Numenius tahitiensis*	Marks (1993)
Rock Pigeon *Columba guinea*	Underhill and Underhill (1997)
Cape Turtle Dove *Streptopelia capicola*	Underhill *et al.* (1999)
Lesser Honeyguide *Indicator minor*	Underhill *et al.* (1995)
Alpine Chough *Pyrrhocorax graculus*	Winkler *et al.* (1988)
Chough *Pyrrhocorax pyrrhocorax*	Winkler *et al.* (1988)
Black-chested Prinia *Prinia flavicans*	Herremans (1999)
Willow Warbler *Phylloscopus trochilus*	Underhill *et al.* (1992)
Common Starling *Sturnus vulgaris*	Cooper and Underhill (1991), Rothery *et al.* (2001)
Sociable Weaver *Philetairus socius*	Oschadleus (2004), chapter 2 of this thesis
Southern Masked Weaver *Ploceus velatus*	Oschadleus *et al.* (2000), Craig *et al.* (2001)
Cape Weaver *Ploceus capensis*	Craig *et al.* (2001)
Village Weaver *Ploceus cucullatus*	Craig *et al.* (2001)
Red-billed Quelea *Quelea quelea*	Craig *et al.* (2001)
Southern Red Bishop *Euplectes orix*	Craig *et al.* (2001)
Greenfinch *Carduelis chloris*	Newton and Rothery (2005)
Bullfinch *Pyrrhula pyrrhula*	Newton and Rothery (2000)

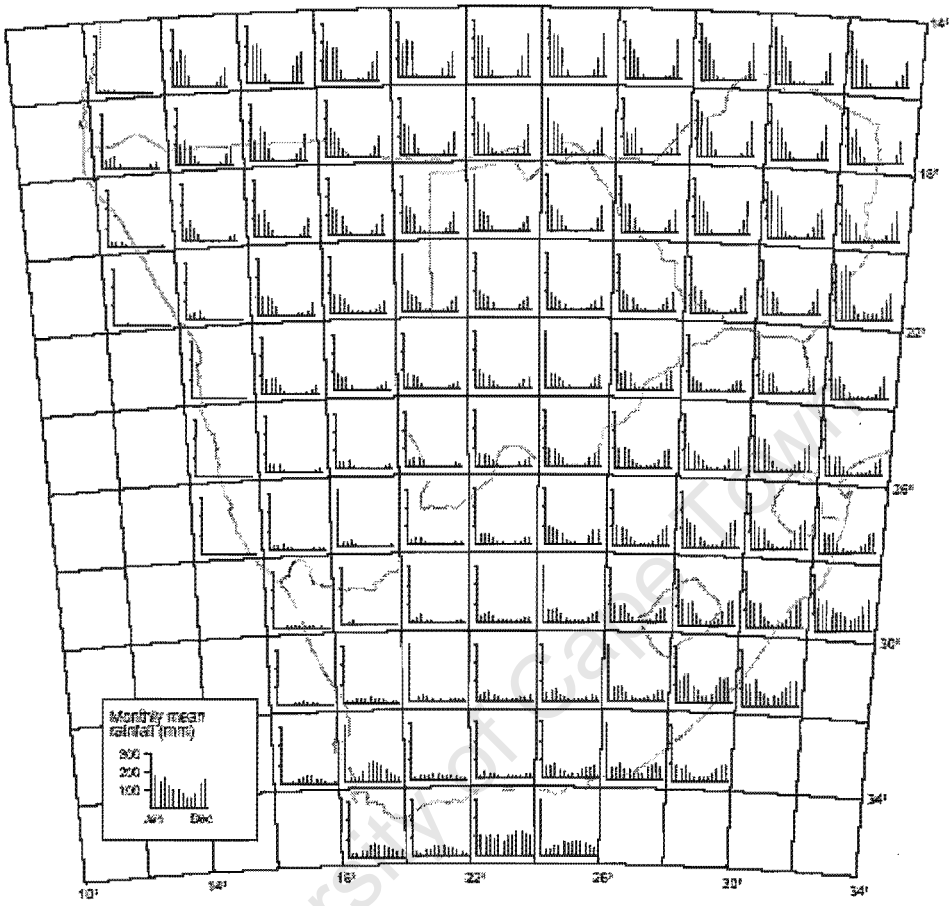
Table 3: Studies of moult in African weavers which did not use the method of Underhill and Zucchini (1987)
GR = Game Reserve, NP = National Park

Species	Area, country	Reference	Comments
Red-billed Buffalo Weaver *Bubalornis niger*	Maun, Botswana	Payne (1969)	Overlap in breeding and moult
White-browed Sparrow-weaver *Plocepasser mahali*	North-western Botswana	Jones (1978)	Duration estimated at 183 days (10 birds); five incubating females were moulting
Chestnut-crowned Sparrow-weaver *Plocepasser superciliosus*	Mole GR, Ghana	Fry (1971)	General notes on breeding and moult
Speckle-fronted Weaver *Sporopipes frontalis*	Mole GR, Ghana	Fry (1971)	General notes on breeding and moult
Scaly-feathered Finch *Sporopipes squamifrons*	Marble Hall, South Africa	Payne (1969)	Overlap in breeding and moult
	Ruretse, Botswana	Tyler (2001)	Moult duration 200–350 days (25 retraps)
Red-headed Malimbe *Malimbus rubricollis*	Kakamega Forest, Kenya	Mann (1985)	Moult score plots (two data points)
Black-billed Weaver *Ploceus melanogaster*	Kakamega Forest, Kenya	Mann (1985)	Moult score plots (four data points)
Black-headed Weaver *Ploceus melanocephalus*	Lake Kanyaboli, Kenya	Britton (1978)	Moult score plots
Black-necked Weaver *Ploceus nigricollis*	Mombasa, Kenya	Britton and Britton (1986)	Moult 5–6 months but varies in individuals
Dark-backed Weaver *Ploceus bicolor*	Somalia	Wood (1989)	Moult in August, none in September
	Pugu Hills, Tanzania	Mlingwa (2000)	Table of some breeding and moult records
Golden Palm Weaver *Ploceus bojeri*	Mombasa, Kenya	Britton and Britton (1986)	Moult 5–6 months but varies in individuals
Heuglin's Masked Weaver *Ploceus heuglini*	Mole GR, Ghana	Fry (1971)	General notes on breeding and moult
Jackson's Golden-backed Weaver *Ploceus jacksoni*	Lake Kanyaboli, Kenya	Britton (1978)	Moult score plots
Lesser Masked Weaver *Ploceus intermedius*	Pugu Hills, Tanzania	Mlingwa (2000)	Table of some breeding and moult records
Northern Brown-throated Weaver *Ploceus castanops*	Lake Kanyaboli, Kenya	Britton (1978)	Moult score plots
Slender-billed Weaver *Ploceus pelzelni*	Mole GR, Ghana	Fry (1971)	General notes on breeding and moult
	Lake Kanyaboli, Kenya	Britton (1978)	Moult score plots
Southern Brown-throated Weaver *Ploceus xanthopterus*	Mopeia, Moambique and Nchalo, Malawi	Hanmer (1984)	Detailed moult study
Spectacled Weaver *Ploceus ocularis*	Mombasa, Kenya	Britton and Britton (1986)	Moult 5–6 months but varies in individuals
	Pugu Hills, Tanzania	Mlingwa (2000)	Table of some breeding and moult records
Vieillot's Black Weaver *Ploceus nigerrimus*	Liberia	Chapman (1995)	This species shows non-seasonal breeding and wet-season moult

Table 3 continued

Species	Area, country	Reference	Comments
Village Weaver *Ploceus cucullatus*	Mole GR, Ghana	Fry (1971)	General notes on breeding and moult
	Lake Kanyaboli, Kenya	Britton (1978)	Moult score plots
	Pugu Hills, Tanzania	Mlingwa (2000)	Table of some breeding and moult records
Thick-billed Weaver *Amblyospiza albifrons*	Pugu Hills, Tanzania	Mlingwa (2000)	Table of some breeding and moult records
	Pietermaritzburg, South Africa	Laycock (1982)	Primary moult duration 4 months
Red-billed Quelea *Quelea quelea*	Tsavo East NP, Kenya	Thompson (1988)	Start moult before breeding completed
Yellow Bishop *Euplectes capensis*	Mt Cameroon, Cameroon	Eyckerman and Cuvelier (1982)	Regression calaculated for 9 birds
Fan-tailed Widow *Euplectes axillaris*	Lake Kanyaboli, Kenya	Britton (1978)	Moult score plots
Yellow-mantled Widow *Euplectes macrourus*	Mole GR, Ghana	Fry (1971)	General notes on breeding and moult
	Kakamega Forest, Kenya	Savalli (1993)	Egg-laying May–September, moult September–November
Zanzibar Red Bishop *Euplectes nigroventris*	Mombasa, Kenya	Britton and Britton (1986)	Moult 5–6 months but varies in individuals
Northern Red Bishop *Euplectes franciscanus*	Mole GR, Ghana	Fry (1971)	General notes on breeding and moult
	Mole NP, Ghana	Davidson (1978)	Prenuptial body moult
Yellow-crowned Bishop *Euplectes afer*	Mole NP, Ghana	Davidson (1978)	Prenuptial body moult
Aldabran Fody *Foudia aldabrana*	Aldabra	Frith (1976)	Post-nuptial moult, April–June
Mauritius Fody *Foudia rubra*	Mauritius	Safford (1997)	Post-nuptial moult, March–April
Seychelles Fody *Foudia sechellarum*	Cousin Island, Seychelles	Brooke (1985)	Breeding follows primary moult

Figure 1: Histograms of mean annual monthly rainfall (mm) for 2° x 2° grid cells in southern Africa (from Allan *et al.* 1997). The plotted data refer to one weather station within the grid cell or are interpolated from neighbouring grid cells, especially in central Botswana.



Chapter 2

Sociable Weaver biometrics and primary moult

Sociable Weaver biometrics and primary moult

Abstract

The biometric and primary moult data housed at the South African Bird Ringing Unit (SAFRING) were analysed for the Sociable Weaver *Philetairus socius*. The average body mass and wing length were 27.9 g (SD 2.2) and 74.1mm (SD 2.5), respectively. Variation in these parameters is not clearly correlated with region, season or climate, other than a negative correlation of body mass with average annual water deficiency. Body mass of Sociable Weavers near Kimberley showed a long-term decrease of 2.9 g, probably due to stabilizing selection on mass. Primary moult duration varied from 152 days to 169 days and started between 26 January and 31 December in two populations (*socius* and South African *eremnus* respectively). Individual primaries moulted mainly one at a time, each taking 20–28 days to grow fully. Prolonged duration of moult in this species is probably an adaptation to reduce energy expenditure, and to grow more durable feathers due to abrasion when entering the nest. The lack of clear patterns of geographical variation in biometrics indicates that the contiguous populations of Sociable Weaver should belong to the nominate subspecies.

Introduction

The Sociable Weaver *Philetairus socius* is a colonial, cooperatively breeding species, best known for its massive communal nests (Craig 2004). It is endemic to the semi-arid savannas of western South Africa, much of Namibia, and south-eastern Botswana (Mendelsohn and Anderson 1997). Breeding is from December to August in northern Namibia, and unseasonal, depending on rainfall, in southern Namibia and in the Northern Cape (Craig 2004). Recently, Craig (2004) considered the species monotypic. However, Clancey (1989) recognised four sub-species of the Sociable Weaver: *P. s. socius, geminus, eremnus* and *xericus*. He considered *P. s. eremnus* to have a disjunct range, being sub-divided by the central nominate subspecies (Figure 1). Clancey (1989) described complex variations in plumage colour throughout the species' range. Compared

to individuals in the centre, weavers at the north and south of the range had darker upperparts and whiter ventral surfaces. These plumage variations were thought to be largely associated with substrate type. Clancey (1989) also found marginal size variation throughout the species' range, thought to be temperature-dependent: birds in the north had shorter wings than those in the south while birds in the south were larger, with a clinal east-to-west increase in wing length.

In this paper, biometric data from Sociable Weavers ringed in South Africa and Namibia are analysed to investigate whether contiguous populations should belong to the nominate sub-species or not. A subset of the records are used to study seasonal and temporal variations in body mass. The timing and total duration of primary moult are also investigated. Sexes are alike and thus the biometrics and moult data are applied to adults (Craig 2004).

Methods

Morphometric data (body mass and wing length) and primary moult data (De Beer *et al.* 2001) for adult Sociable Weavers were obtained from records submitted between 1970 and May 2004 to SAFRING. Body mass and wing length data were analysed according to the subspecies distribution map in Clancey (1989), and on a finer scale by degree grid to investigate geographic variation. A degree grid cell is 1° x 1°, e.g. 1915 is the one degree grid cell with 19°S 15°E in the north-western corner. Spearman's rank correlation co-efficient was used to compare body mass and wing length to rainfall, temperature and water deficiency (extracted from Schultze and McGee 1978) by grid cell. Water deficiency is the moisture needed by vegetation that soil water storage and rainfall cannot supply, and is an indicator of drought or aridity (Schultze and McGee 1978).

A comprehensive subset of mass records was obtained from Benfontein Game Farm, 6 km south-east of Kimberley, Northern Cape, South Africa (approx. 28°53'S 24°49'E, see Covas *et al.* 2002 for study area details). To investigate temporal variation in mass, the weighted moving average method developed by Cleveland (1979) and implemented, for example, by Summers *et al.* (1992), was used. This algorithm enables a smooth curve to be fitted to the scatterplot of mean body mass against date. This method

does not have discontinuities as happens in the usual moving average or moving window smoothing methods, because individual points are included and then excluded from the moving average. Rainfall models were applied to compare with body mass, using combinations of rainfall in the current and previous months. Monthly rainfall for 1993 to 2003 was obtained from Kimberley Airport (about 15 km from Benfontein Game Farm).

To determine the mass of primary feathers, individual feathers from three wings of two Sociable Weaver specimens were oven-dried at 60°C for 24 hours and then weighed on a balance (Ohaus GA200D, precision 0.0001g) (compare Underhill and Summers 1993). Underhill and Joubert (1995) have shown that small samples are adequate to determine the relative masses of primary feathers, because there is little intra-specific variation in this characteristic. The Underhill-Zucchini moult model (Underhill and Zucchini 1988) was applied to the data sets. The data were considered to be of 'type 2' because Sociable Weavers remain near their nests, and are available for capture throughout the year (Mendelsohn and Anderson 1997). The parameters of primary moult were estimated using the transformations recommended by Summers *et al.* (1980, 1983), designed to reduce the bias introduced by the fact that the individual feathers are of different masses. The moult index used was percentage feather mass grown (PFMG), calculated according to the method of Underhill and Summers (1993). The Underhill-Zucchini model was also used to estimate the parameters of moult for individual primary feathers, as done for selected species of waders by Underhill (2003).

Results

The following analyses are based on 4895 ringing records and 3069 recapture records of 7964 adult Sociable Weavers, sampled throughout most of the species' distribution range (Figure 1). The records contained at least body mass, or wing length, or primary moult information.

Geographic and seasonal variation in body mass and wing length

Mean body mass was 27.9 g (SD=2.2, range=18–39.6, n=7846) and mean wing length was 74.1 mm (SD=2.5, range=64–84, n=5940).

The mean body mass and wing length were calculated for each subspecies (Table 1). A one-way ANOVA on the ringing data showed that the mean masses of the five groups had a range of 2.8 g, with individuals of the *eremnus* population in South Africa being the heaviest (mean mass 28.6 g), and individuals of the Namibian population of this subspecies being the lightest (mean mass 25.8 g) of all five groups. These differences were statistically significant ($F_{4,\ 7841} = 416.8$, $P<0.001$). There was a similar pattern for wing length, with *eremnus* individuals having a longer wing than individuals of other populations ($F_{4,\ 5935} = 455.8$, $P<0.001$) (Table 1). Wing lengths obtained from ringing data were smaller than Clancey's (1989) museum specimen data (Table 1).

To investigate geographic variation in body mass in more detail, and independently of Clancey's subspecies, the mean masses per degree grid cell were calculated (Table 2). A one-way ANOVA showed significant variation ($F_{15,\ 7286} = 131.2$, $P<0.001$), with individuals in grid 2824 (part of the *eremnus* population in South Africa) being the heaviest (mean mass 28.7 g), and individuals in grid 2315 (part of the *eremnus* population in Namibia) being the lightest (mean mass 24.1 g). Similarly, significant variation was obtained for wing length ($F_{8,\ 5400} = 222.7$, $P<0.001$), although the largest wing length was in grid 2821 (part of the *socius* population). Tabulating the difference of the mean mass or wing length per grid from the overall mean did not, however, show any obvious pattern (Table 2).

Mean body mass, wing length, annual rainfall, temperature and annual water deficiency were averaged for each grid cell (14 in total) to determine whether there is a change in body mass or wing length with increasing aridity. There was no significant correlation between wing length and mean annual rainfall ($r_s = 0.36$, $p>0.05$), mean annual temperature ($r_s = 0.13$, $p>0.05$), or average annual water deficiency ($r_s = -0.26$, $p>0.05$). Similarly, there was no significant correlation between body mass (number of grid cells =19) and mean annual rainfall ($r_s = 0.14$, $p>0.05$) or mean annual temperature ($r_s = -0.24$, $p>0.05$). There was, however, a significant negative correlation between body mass and average annual water deficiency ($r_s = -0.43$, $p<0.05$).

For *eremnus* (South Africa), body mass varied from 28g to 30g and no clear seasonal pattern was evident (Figure 2). Full sets of monthly data were not available for the other subspecies. However, mean monthly masses of *P. s. eremnus* (Namibia) were

generally lower than those of *eremnus* (South Africa) (Figure 2). The incomplete data sets available for the other subspecies indicated wide fluctuations in mean monthly mass, and this was greatest for *P. s. socius* (24 to 28 g) (Figure 2).

Temporal changes in body mass at Benfontein Game Farm

Plotting the means of the mass data for adult Sociable Weavers at Benfontein over 10-day intervals showed a long-term decline (Figure 3) from a mean mass 29.1g (SD=1.9, n=3039) between August 1992 and June 1998, to 27.9 g (SD=1.8, n=1214) between November 1998 and September 2001, to 26.3 g (SD=1.9, n=365) between September 2002 and December 2003. This represented a reduction in mean mass of 2.9 g (9.9%) between the first and last periods considered here. Two ringers were involved during the first two periods but inter-observer difference in mean mass (29.2 and 28.7 g) was only 0.5 g. During the third period a third ringer was involved with no recaptures so it is not possible to check for inter-observer differences.

The influence of monthly rainfall on mean monthly mass at Benfontein was investigated. Several models were tested, each using the change in mean mass in the current month m_i and the next month m_{i+1}. Mass changes (m_{i+1} — m_i) relative to rainfall were modelled using four rainfall indices: (a) rain in current month r_i (b) rain in previous month r_{i-1} (c) sum of rain in current month and previous month $r_i + r_{i-1}$ and (d) rain in current month $r_i > 0$ and rain in previous month $r_{i-1} = 0$, to see the effect of rain after a dry month. In each model, the linear regression was not significant. A second order polynomial fit gave a curve starting near zero and dropping slightly below zero with increasing rainfall, before increasing at very high rainfall (example of model (a) in Figure 4; the quadratic equation shown is not significant).

Timing and duration of primary moult

Individual primaries from two Sociable Weaver museum specimens were weighed (Table 3). The Sociable Weaver has 10 primary feathers, but the 10th primary is vestigial. This outermost primary had a mass less than 0.0001 g, and was thus not considered in moult calculations. The innermost primaries accounted for 8.5–11.6% each of the total mass of the primary feathers. Primaries 6–8 were the largest, and similar in size, accounting for

12.4–12.7% of the relative primary mass. 1733 ringing and recapture records with primary moult information were extracted. 18 records showed irregular moult, i.e. a pattern not ascendant, e.g. 155553000. 128 records (7.4% of total) showed apparent suspended moult, e.g. 555555000. By subspecies, the numbers of birds showing suspended moult were *P. s. eremnus* 18 (1.0%), *geminus* 38 (2.2%), and *socius* 70 (4.0%). One bird (BH00041) had apparently suspended moult after its fourth primary was renewed, and had recommenced moult from the fifth primary (score 888855520). Unlike birds that moult more than one primary simultaneously, it was not apparent if moult was suspended or recorded just before the next primary was dropped. The irregular and suspended moult data were not included in further analyses.

50.0% of 1586 remaining records indicated active moult (i.e. at least one feather with a score between 1 and 4). 22 records had at least three feathers scored as 4, e.g. 444441000, and one record with three feathers scored as 3. Frequency of number of growing primaries of those in moult was one (82.1%), two (13.2%), three (1.3%) and four (0.3%) feathers. Thus 82.2% of Sociable Weavers have one primary in active moult when moulting, with less than 15% of birds growing more than one primary feather at a time.

Three recaptures at Benfontein within the same year with capture dates near start and end of moult gave the following extrapolated results: 136 days duration starting on 16 February, 281 days duration starting on 9 November and 337 days duration starting on 4 December. For the South African *eremnus* population (Benfontein data, plus two records from Sandveld Nature Reserve; Figure 5) duration of moult was 169 days (5.6 months) and the average starting date was 31 December. 83% of records were from 1996 and 2000. There were sufficient data to analyse moult in a single year for *eremnus* at Benfontein in 1996 and this was similar for the moult analysis with the data from all years (Table 4). In *socius* (Northern Cape, 13 sites in degree grid 2821), duration of moult was 152 days (5.1 months) and started on 26 January. 88% of records were from 2000 and 2002 (Table 4). In *geminus* (northern Namibia), duration of moult was 216 days (7.2 months) and started on 28 January; however, most of these data were collected at the start of the moult so that the duration and end dates have larger standard errors and are less reliable than the start date (Table 4).

Applying the Underhill-Zucchini model to individual primary feathers gave results for primaries 3–9; there were insufficient data for primaries 1 and 2 for the algorithm to converge. Individual feathers took 20–28 days to grow (Table 5). The timing of moult for primaries 3–6 showed no or little overlap, i.e. only one feather growing at a time. Later primaries showed increasing overlap (Figure 6), rather than speeding up individual growth feather rates.

Discussion

Geographic and seasonal variation in body mass and wing length

Clancey (1989) considered complicated patterns of size variation, based on small sample sizes of museum specimens of Sociable Weavers. He considered wing length to increase from north to south, and east to west. Analysing ringing data by subspecies indicates that body mass and wing length are smaller in *eremnus* (Namibia) and *geminus*, lending possible support for a north-to-south increase in size. There is no clear pattern from east to west (Table 1): based on ringing data, the largest individuals belong to *eremnus* (South Africa) rather than *xericus*, as suggested by Clancey (1989). Analysis by degree grids also shows geographical variability in body size. However, this variation may be an artefact of data collection methods. For example, some grid cells were represented by small sample sizes, data from some samples were collected on only one day, and measurements were performed by different ringers. One grid cell had 4816 records and it was thus inevitable that high levels of statistical significance would result although these would not necessarily be biologically meaningful (Underhill 1999).

Surprisingly Clancey's (1989) wing lengths are longer than those calculated from the ringing data (Table 1). Museum specimens shrink, giving shorter measurements than from live birds (Herremans *et al.* 1999, and references therein). Ringers use maximum wing chord measurement (de Beer *et al.* 2001), so Clancey's longer wing measurements are not readily explained. Herremans *et al.* (1999) obtained a similar result for Levaillant's Cisticola *Cisticola tinniens* and considered biometrics based on small samples of museum specimens to be misleading. They recommended that large samples of measurements of live birds should be used.

The only significant correlation between biometric measurements and environmental indices was the negative correlation of body mass with average annual water deficiency. Bergmann's rule states that warm-blooded vertebrates from cooler climates tend to be larger than congeners from warmer climates, but evaporation should be included in the climatic variable (see Meiri and Dayan 2003), which could explain why a correlation was found with water deficiency and not the other variables.

There was variation in mean monthly body mass of adult Sociable Weavers in different regions of southern Africa. These were not clearly correlated with season, and were probably attributable to the underlying data being collected in different years and months in different localities.

Temporal changes in body mass at Benfontein

For Benfontein there were sufficient data to look at body mass changes in more detail, over seasons and years. After rainfall events, breeding is initiated as a result of the increased availability of invertebrates that are fed to the chicks (Maclean 1973). The lack of correlation between mean monthly body mass and rainfall in this study indicates that Sociable Weavers at Benfontein expend energy on reproduction rather than increasing adult body mass when food increases.

There was a long-term decline in mean mass of 2.9 g (<10%). This might be an artefact of sampling effort, with birds during the latter years only being weighed during the breeding season. This seems unlikely since there was little seasonal variation in mass. Inter-observer differences in weighing the birds does not explain the slight decline between the first two periods, but cannot be tested for the last period. Sociable Weavers differ in mass by about 3g (11%) between evening and morning (Spottiswoode *in litt.*), which is similar to the overnight mass loss of 6–13% recorded for three other weaver species (Oschadleus 2001). Time of capture or ringing is not recorded in the SAFRING database but most Sociable Weavers at Benfontein were captured at sunrise (Covas 2002: 44). Thus the effect of daily mass loss is minimised, except where large numbers of birds were captured, resulting in delay between capture and processing and thus possible changes in body mass. Other possibilities for temporal mass changes are due to global warming (e.g. Yom-Tov 2001), but the change recorded here is probably over too short a

term for this explanation to apply. Covas *et al.* (2002) showed that there is a strong stabilizing selection on body mass, verifying the prediction that body mass probably results from a trade-off between the risks of starvation at low mass and predation at high mass (Gosler and Greenwood 1995). While the data may be affected to some extent by the biases noted, the consistent long-term decline in mass of Sociable Weavers at Benfontein is more likely due to stabilizing selection. Whether this is due to changes in food supply or in predation rates requires further investigation.

Timing and duration of primary moult

The life history of Sociable Weavers is largely influenced by a benign climate, which leads to reduced mortality; this should favour reduced fecundity (Covas 2002). Food availability determines if breeding can occur (Covas 2002). Individuals should thus optimise energy requirements between breeding and moult by breeding when sufficient food is available and by moulting flight feathers at a relatively slow rate.

In some species of Ploceidae, e.g. Chestnut Weavers *Ploceus rubiginosus*, timing of moult is fairly consistent between years despite variations in rainfall and thus breeding season (Komen and Buys 1990). On the eastern margin of the Sociable Weavers' range, the breeding period generally begins in spring (late-August to September) (Covas 2002), although its onset depends on rainfall and varies considerably between years (Maclean 1973). Breeding may be entirely absent during drought years (Maclean 1973) but may continue for nine months in wet years (Maclean 1973, Covas 2002). Moult in this species appears to commence between the end of December and January. Breeding may thus overlap with an extended moult season (Spottiswoode *in litt.*), and primary moult may be interrupted during intense breeding periods (Maclean 1973).

Ploceidae in semi-arid environments have widely varying moult durations, although data have not been analysed rigorously. Adult Chestnut Weavers in northern Namibia moult their primaries from June to September, i.e. in about 120 days (Komen and Buys 1990). The duration of primary moult in White-browed Sparrow-weavers *Plocepasser mahali* is 183 days (Jones 1978). Primary moult in Scaly-feathered Finches *Sporopipes squamifrons* is slow, with an estimated duration of *c.* 200–350 days (Tyler 2001). Other avian taxa in arid areas also have prolonged primary moult periods, e.g.

sandgrouse moult over eight months in Tanzania (Kalchreuter 1979). The moult in most of 20 species of arid-zone birds studied in Australia lasted 4–4.5 months (Keast 1968). Dean (2004) reviewed duration of moult in arid nomadic species, concluding that duration is highly variable.

For Sociable Weavers, Maclean (1973) noted that about one primary was replaced per month, with the shortest recorded time being three weeks. Individual primaries moult mainly one at a time and need 20–28 days to grow, but the last three primaries show increasing overlap in their growing period, reducing the total duration of primary moult. Maclean's (1996) estimate of nine months for primary moult is thus exaggerated. The present study indicated moult durations of 5.1–7.2 months, longer than the moult durations of weavers in the moister eastern parts of southern Africa where moult lasts from three to four months (Craig *et al.* 2001). The three recapture estimates for moult duration varied widely but could have been due to suspended moult. A long primary moult may be an adaptation to reduce energy expenditure since primary productivity is low in semi-arid environments (Tieleman 2002). In addition, slow-growing primaries are more resistant to abrasion than fast-growing ones (Dawson *et al.* 2000). Sociable Weaver feathers may experience high rates of feather abrasion when entering and leaving their nests, as their aluminium rings wear away relatively quickly compared to stainless steel rings (Nuttall 2001). Slow-growing high quality primaries would then reduce the abrasive effect of the stiff grasses projecting along the nest entrances. Using individual primary feather analyses gives additional insights into duration of moult. For example, it was not previously known that Sociable Weavers overlap in the moult of the last three primaries. The only comparable analysis of the moult of individual primary feathers is for waders, where several feathers frequently grow simultaneously (Underhill 2003).

The relative primary feather masses measured in this study, each ranging between 8.5–12.7% of the total primary feather mass, are typical of a non-migratory species and are similar to that of other weavers (Underhill and Joubert 1995, Craig *et al.* 2001).

Subspecies of the Sociable Weaver

Clancey (1957) described *eremnus* as a new subspecies in the Northern Cape. Later, Clancey (1989) included a Namibian population within the range of *eremnus*, without

adequate justification. In fact, he admits that a long series taken in Namibia 'contain many specimens intermediate between nominate *socius* and *eremnus*...' (Clancey 1989: 231). Although differences do exist, for instance the smaller birds in northern Namibia, it is best to consider the contiguous Sociable Weaver populations to be monotypic. Craig (2004) also considered the species monotypic, as regional differences are not consistent.

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Table 1: Mass (g) and wing measurements (mm) of adult Sociable Weavers in southern Africa, from ringers' data by Sociable Weaver population, compared with data from Clancey (1989)
eremnus (SA) = *eremnus* population in South Africa
eremnus (Namibia) = *eremnus* population in Namibia

	eremnus (S Africa)	*eremnus (Namibia)*	*geminus*	*socius*	*xericus*
Mass (g)					
Mean	28.6	25.8	26.7	27.1	27.4
Range	20.5–39.6	20.0–33.0	20.7–39.0	18.0–36.0	20.5–33.7
Standard deviation	2.0	1.7	2.0	2.3	1.8
n	4915	514	991	1087	339
Wing (mm)					
Mean	75.0	72.9	72.0	73.0	74.1
Range	68–81.5	66–78	64–84	65–80	69–82
Standard deviation	2.2	2.3	2.0	2.2	1.9
n	3644	239	931	991	135
Wing (mm), summarised from Clancey (1989)					
Mean	75.6	73.7	73.7	75.4	78.5
Range	72.5–79	71–75.5	72–75.5	71.5–80	75.5–81
Standard deviation	–	1.43	1.28	–	1.94
n	34	10	8	55	6

Table 2: Mass (g) and wing measurements (mm) of adult Sociable Weaver populations in southern Africa, from ringers' data, averaged by degree grids (e.g. 1915 = refers to the one degree grid cell with 19°S 15°E in the north western corner)
eremnus (SA) = *eremnus* population in South Africa
eremnus (Namibia) = *eremnus* population in Namibia

Degree grid	Population	Mean mass (g)	Range (g)	Standard deviation	n	Difference from overall mean
2725	*eremnus (SA)*	27.5	22–36	1.8	525	–0.4
2824	*eremnus (SA)*	28.7	20.5–39.6	2.0	4390	0.8
2118	*eremnus (Namibia)*	26.1	25–27	0.8	8	–1.8
2216	*eremnus (Namibia)*	25.9	20–33	1.7	338	–2.0
2315	*eremnus (Namibia)*	24.1	22–29	1.6	26	–3.8
2317	*eremnus (Namibia)*	26.1	22.7–31	1.5	142	–1.8
1915	*geminus*	26.7	20.7–39	2.0	991	–1.2
2420	*socius*	24.5	23–26.2	1.1	10	–3.4
2520	*socius*	26.4	–	–	1	–1.5
2618	*socius*	25.9	23–29	1.3	29	–2.0
2721	*socius*	24.2	18–30	1.7	117	–3.7
2821	*socius*	27.2	26–28.5	1.3	3	–0.7
2822	*socius*	27.5	19.2–36	2.2	840	–0.4
2823	*socius*	28.5	26.5–30	1.8	3	0.6
2921	*socius*	28.2	26–31	1.3	84	0.3
2415	*xericus*	27.4	26–30	1.2	15	–0.5
2416	*xericus*	27.4	23–32	1.8	88	–0.5
2516	*xericus*	27.5	20.5–33.7	1.9	191	–0.4
2616	*xericus*	26.8	21–29	1.5	45	–1.1
All mass		27.9	18-39.6	2.2	7846	

Degree grid	Population	Mean wing (mm)	Range (mm)	Standard deviation	n	Difference from overall mean
2725	*eremnus (SA)*	73.8	71–78	1.8	16	–0.3
2824	*eremnus (SA)*	75.0	68–81.5	2.2	3628	0.9
2118	*eremnus (Namibia)*	75.4	73–77	1.3	8	1.3
2216	*eremnus (Namibia)*	72.8	68–76	1.9	56	–1.3
2315	*eremnus (Namibia)*	69.4	66–73	1.3	28	–4.7
2317	*eremnus (Namibia)*	73.4	68–78	2.0	147	–0.7
1915	*geminus*	72.0	64–84	2.0	931	–2.1
2618	*socius*	71.6	67–76	1.9	30	–2.5
2721	*socius*	71.4	68–76	1.3	113	–2.7
2821	*socius*	76.8	76–77	0.5	4	2.7
2822	*socius*	73.2	65–80	2.2	841	–0.9
2823	*socius*	76.0	72–79	3.6	3	1.9
2516	*xericus*	74.0	69–82	2.1	94	–0.1
2616	*xericus*	74.3	72–77	1.5	41	0.2
All wing		74.1	64-84	2.5	5940	

Table 3: Individual primary feather masses (g) of two Sociable Weaver specimens from Kimberley, Northern Cape, and the mean relative mass of each primary, used in the calculation of Percentage Feather Mass Grown

Primary	Feather mass (g)			Mean relative feather masses
	Bird 1 left wing	Bird 2 left wing	Bird 2 right wing	
1	0.0098	0.0101	0.0100	8.5
2	0.0103	0.0110	0.0107	9.1
3	0.0113	0.0117	0.0120	10.0
4	0.0127	0.0127	0.0128	10.9
5	0.0136	0.0133	0.0136	11.6
6	0.0139	0.0147	0.0154	12.6
7	0.0142	0.0145	0.0148	12.4
8	0.0147	0.0147	0.0151	12.7
9	0.0136	0.0142	0.0149	12.2
10	<0.0001	<0.0001	<0.0001	0.0
Total	0.1141	0.1169	0.1193	100.0

Table 4: Estimates of the primary moult parameters for adult Sociable Weavers in southern Africa
eremnus (SA) = *eremnus* population in South Africa

Subspecies	Mean starting date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Duration (months)	Standard error (days)	Mean completion date	Standard error (days)	n
eremnus (SA)	31 Dec	6.1	38.0	2.2	168.9	5.6	8.1	17 Jun	3.7	481
eremnus (SA), 1996	24 Dec	7.9	28.4	2.1	176.4	5.9	10.0	17 Jun	3.4	204
geminus	28 Jan	5.9	67.5	5.0	215.8	7.2	13.8	31 Aug	12.0	231
socius	26 Jan	4.1	37.7	1.9	151.7	5.1	7.2	26 Jun	3.8	838

Table 5: Moult parameters of individual primary feathers for adult Sociable Weavers of the *eremnus* (South Africa) population

Primary	Mean starting date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Standard error (days)	Mean completion date	Standard error (days)
3	9 Jan	9.5	33.8	5.6	20.4	6.4	29 Jan	7.2
4	1 Feb	4.8	22.5	2.7	25.7	4.8	26 Feb	3.7
5	28 Feb	4.8	32.2	3.4	27.7	4.6	27 Mar	3.7
6	29 Mar	3.9	33.1	3.2	24.3	3.9	22 Apr	3.6
7	21 Apr	3.3	28.2	2.6	21.2	3.5	12 May	3.4
8	8 May	3.0	23.4	2.1	22.6	3.5	30 May	3.2
9	24 May	2.9	20.1	1.9	26.9	3.7	20 Jun	3.0

Figure 1: Distribution of Sociable Weavers in southern Africa, showing the races described by Clancey (1989) where s = *P. s. socius,* g = *geminus,* e = *eremnus* (South African population), en = *eremnus* (Namibian population) and x = *xericus*; large dots indicate ringing sites with at least mass or wing or primary moult data

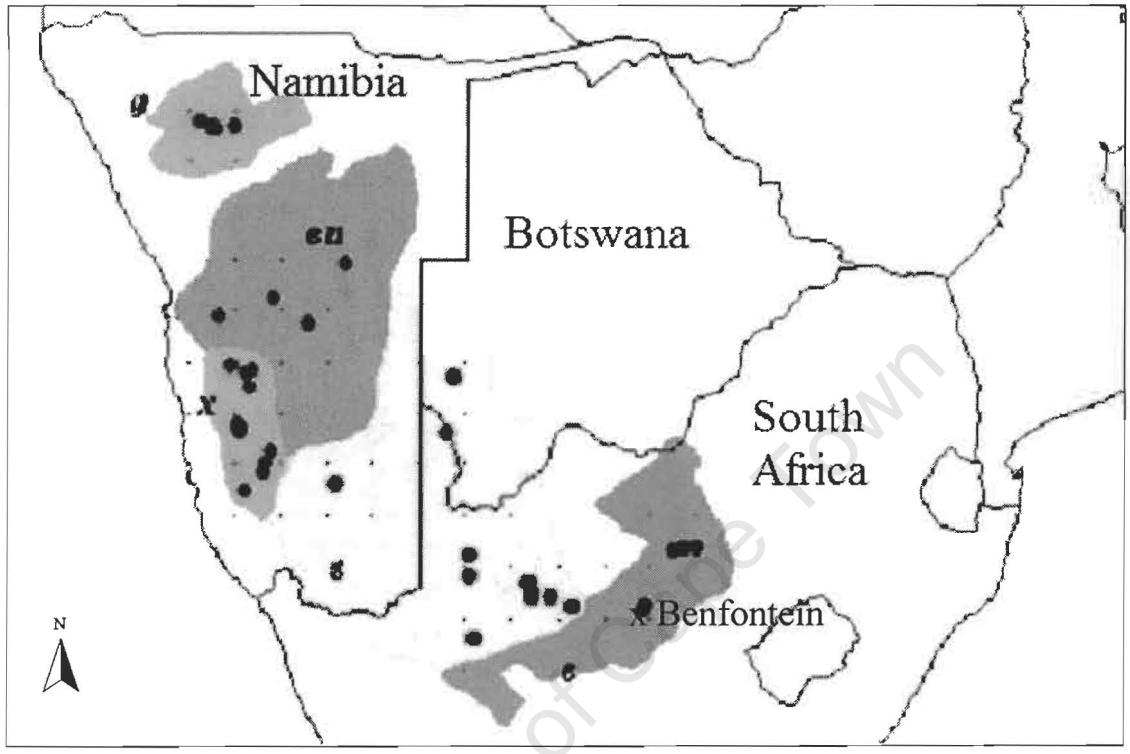


Figure 2: Mean mass per month for five populations of Sociable Weavers in southern Africa, all years combined; subspecies as described by Clancey (1989) where *P. s. socius,* solid squares; *geminus,* open squares; *eremnus* (South African population), open triangles; *eremnus* (Namibian population), solid triangles; and *xericus*, crosses

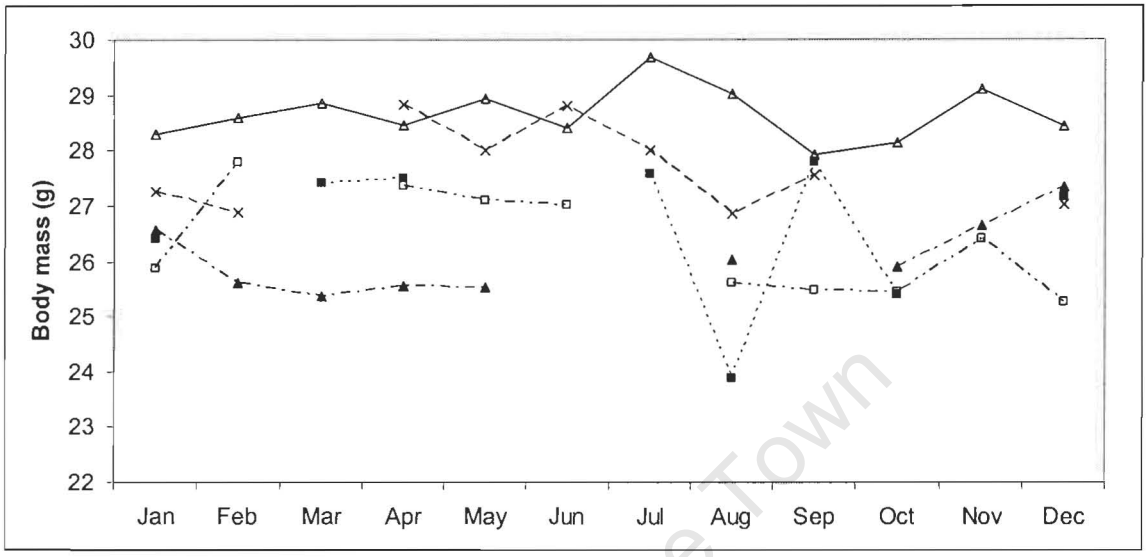


Figure 3: Mean mass per 10-day period for adult Sociable Weavers at Benfontein, Northern Cape

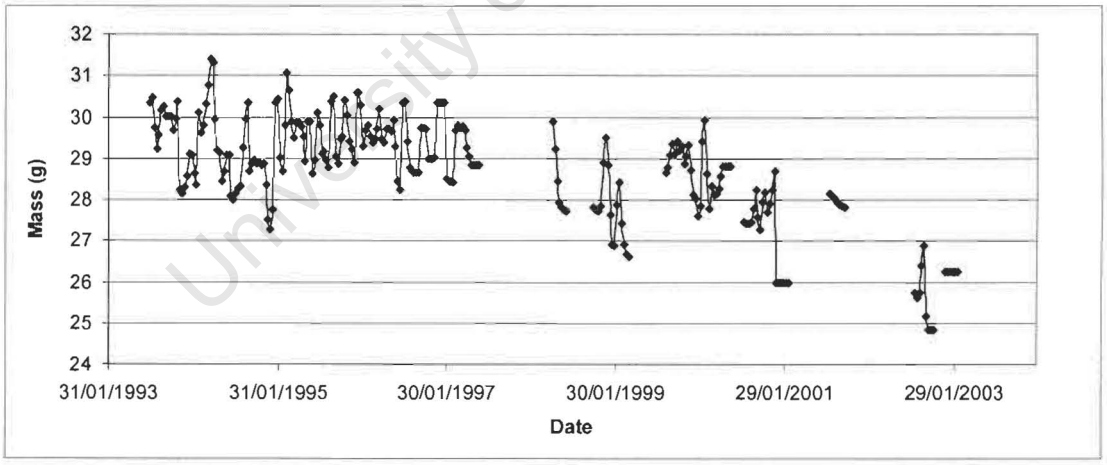


Figure 4: Mass change versus rainfall for adult Sociable Weavers at Benfontein, Northern Cape; model (a) – see text

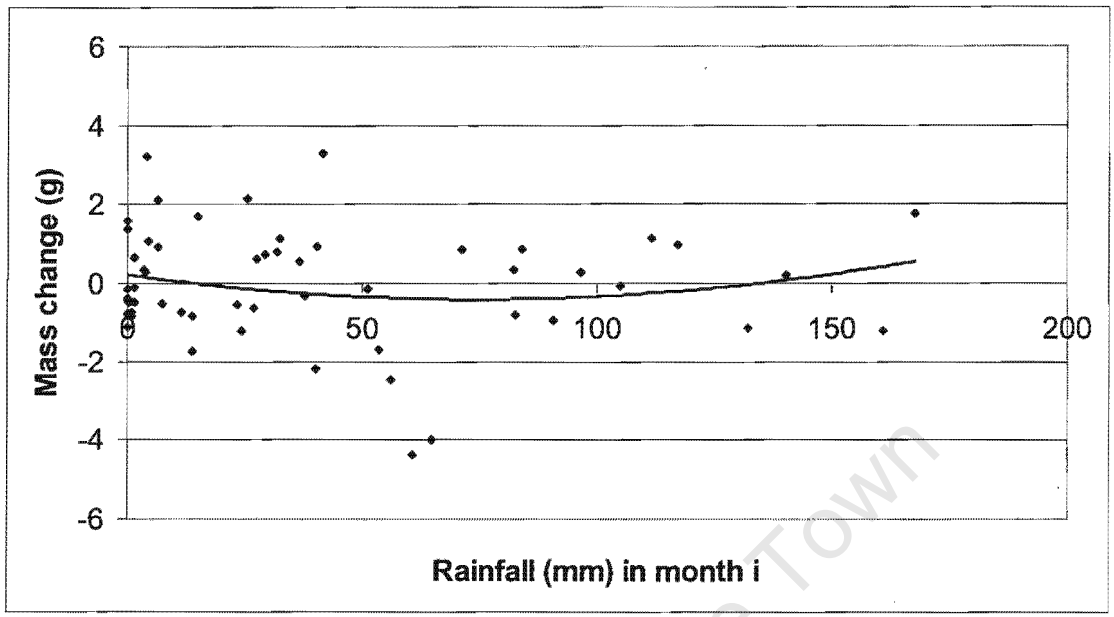


Figure 5: Timing of primary moult for adult Sociable Weavers of the *eremnus* (South Africa) population; the solid diamonds represent relative feather mass values by date; the solid diagonal line joins the estimated mean start and end dates of moult, while the diagonal dotted lines show the approximate 95% confidence intervals of moult scores on any given date

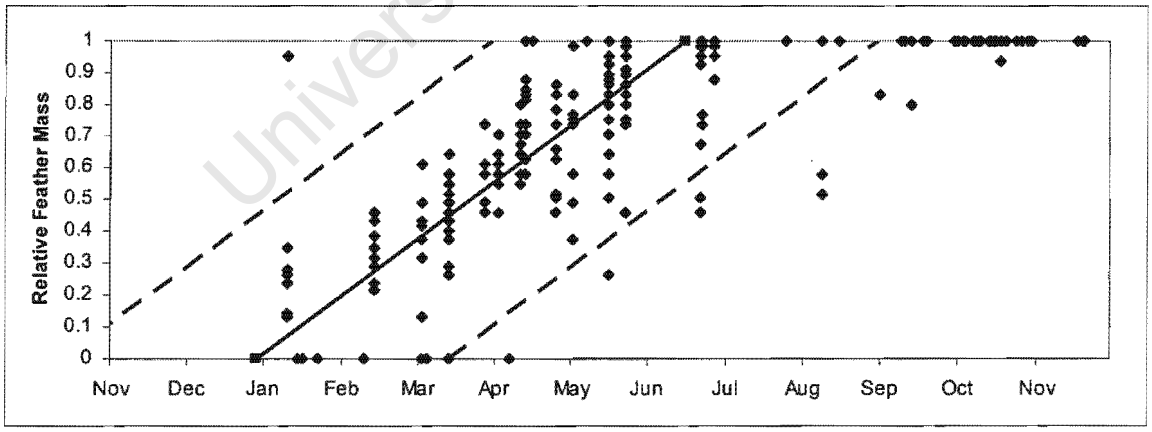
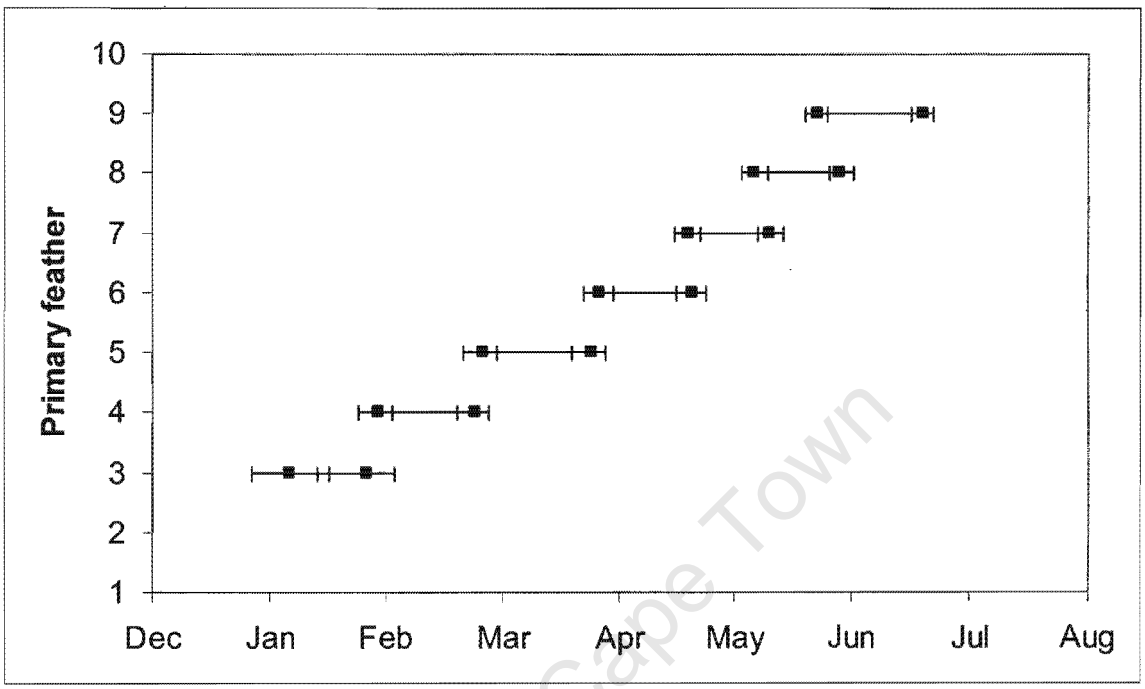


Figure 6: Individual primary growth of adult Sociable Weavers of the *eremnus* (South Africa) population; start and end of primary growth (and standard deviation) for primaries 3–9 are shown (insufficient data for primaries 1 and 2); data in Table 5



Chapter 3

Chestnut Weaver biometrics and primary moult in Namibia

Chestnut Weaver biometrics and primary moult in Namibia

Abstract

Seasonal variation in body mass and wing length, and the onset and duration of primary moult, were investigated for Chestnut Weavers from northern Namibia. Body mass of adult males was 31.2 g (SD 2.6) and adult females weighed 27.4 g (SD 1.9). Body mass declined from March to April, and started increasing after August (i.e. near the end of moult) in males and females. Wing length in adult males with new primaries (October – February) was 80.7 mm (SD 2.7) and for adult females (October – February) 76.8 mm (SD 2.6). For both sexes wing length declined during and after the breeding season due to extensive feather wear. Adult males started primary moult significantly earlier than females (9 April versus 30 April) and moult lasted longer (206 days versus 189 days). The peak summer rainfall and the start of primary moult were earliest in 2000 and latest in 2004 for males and females. Individual primary feathers took 11 to 18 days to grow.

Introduction

The Chestnut Weaver *Ploceus rubiginosus* is a colonial species of arid regions. It is a local migrant or seasonally nomadic. There are two discrete populations: *P. r. trothae* occurs in northern Namibia, Botswana and southern Angola and the nominate subspecies in eastern Africa in Eritrea, Ethiopia, Somalia, Uganda, Kenya and Tanzania (Craig 2004). In Namibia, this species breeds mostly in the open semi-arid savanna of the Namibian escarpment (Herremans 1997).

In Namibia the Chestnut Weaver has a single breeding season during the wet season, thus breeding can occur anytime from December to May, with a peak in February – March (Herremans 1997). It is not known whether this species makes more than one breeding attempt in any one breeding season (Komen and Buys 1990). Males build the nests, copulate with receptive females and then desert the colony soon afterwards, leaving the females to incubate the eggs and rear the young (Komen and Buys 1990). Nest building takes about four days (Halenke 1971), incubation is 11–14 days and fledging 13–16 days (Craig 2004), giving a breeding cycle of 28–34 days.

Adult wing-moult begins between April and June, and is completed by October (Komen and Buys 1990). Komen and Buys (1990) showed that males initiate moult earlier than females because males can start moult when they have left the colonies, but breeding females must continue caring for their young before they are able to start moult. However, the starting date of moult, the duration of moult and the delay between the starting date of females relative to males, are unknown. The aim of this paper was to provide these data on moult, and on the seasonal variation in body mass and wing length, for Chestnut Weavers in Namibia.

Methods

Ringing data were collected in the standard SAFRING (South African Bird Ringing Unit) electronic format. This includes standard ringing information (such as location and date) and data on bird body mass, wing length and primary moult (de Beer *et al.* 2001). Records were from the degree grid cell 19°S–20°S, 15°E–16°E, mostly on Windpoort Farm (19°20'S 15°28'E), Namibia (Figure 1). Birds were sexed on plumage in the breeding season, and on a combination of features like general size, eye colour, bill length and shape, and leg size during the non-breeding season. Body mass and wing length data were analysed by sex and by month. Monthly rainfall data were recorded on Tandala Ridge on Windpoort Farm.

The Chestnut Weaver has 10 primary feathers, moulted from the innermost primary outwards. The primaries of four wings from two female specimens and two wings of a male specimen were dried in an oven at 60°C for 24 hours to eliminate moisture and weighed (Ohaus GA200D balance, precision 0.0001g), to determine the relative mass of each primary (as described in Underhill and Summers 1993). Underhill and Joubert (1995) showed that small samples are adequate to determine the relative masses of primary feathers because there is little intra-specific variation in this characteristic. The Underhill-Zucchini moult model (Underhill and Zucchini 1988), developed to estimate start and duration of primary moult, was applied to the data sets. The data were considered to be of 'type 2' of Underhill and Zucchini (1988), because full moult scores were recorded for each bird and all birds were considered available for sampling throughout the moult period. The parameters of primary moult were estimated using the transformations recommended by Summers *et*

al. (1980, 1983), designed to reduce the bias introduced by the fact that the individual feathers are of different masses. The moult index used was percentage feather mass grown (PFMG), calculated from the moult score for the individual feathers according to the method of Underhill and Summers (1993). In addition, this analysis was undertaken to estimate the parameters of moult of each primary (Underhill 2003, Underhill *et al.* in press).

Brandao (1998) (see also Underhill *et al.* in press) extended the Underhill-Zucchini (1988) moult model to estimate starting dates for groups of birds (e.g. males and females, or annual groups), holding the other two parameters (duration and standard deviation) constant. She also developed rigorous statistical testing, using the likelihood ratio test, of the null hypothesis that the starting date for each group was the same. This method was applied to analyse inter-annual variation in moult and to estimate starting dates for males and females in different years.

Results

1560 ringing records and six recapture records were obtained for adult Chestnut Weavers of known sex between April 1999 and November 2004.

Sexual and seasonal variation in body mass and wing length

The mean masses of adult male and female Chestnut Weavers were 31.2 g (SD 2.6) and 27.4 g (SD 1.9) respectively (Table 1). Mass declined after the breeding season and started increasing at the end of moult, in both males and females (Figure 2). The peaks in body mass in March, September and December may be due to the small sample sizes ($n<30$ in each of these months for both sexes).

Wing length was analysed for birds with new primaries (October – February), giving 80.7 mm (SD 2.7) and 76.8 mm (SD 2.6) for adult males and females, respectively (Table 1). Wing length declined after the breeding season in both males and females (Figure 3), presumably due to abrasion of feather tips. The extent of feather abrasion is estimated by the difference between the minimum monthly average (in June, Figure 3) and the length of wings with new primaries. The average decreases in wing length were 5.8 mm and 4.6 mm for males and females respectively (Figure 3). Most of this abrasion took place during and immediately after the breeding season.

Timing and duration of primary moult

Relative primary feather masses of males was heavier in males than females for primaries 1-5, equal in primary 6 and heavier in females than males for primaries 7-10 (Table 2).

Records of four males and four females indicated arrested moult because there were new primaries followed by old primaries (one bird in April, one in May, two in July, four in August) and these were excluded from this analysis. Of birds in moult the number of growing primary feathers in an individual was one (92.0%), two (7.8%), and three (0.2%).

Moulting birds were captured throughout the moulting season (Figures 4 and 5); this enables the moult parameters to be estimated reliably. For adult males, duration of moult was estimated to be 206 days (6.9 months) and the mean starting date was 9 April. For adult females, duration of moult was estimated to be 189 days (6.3 months) and the mean starting date was 30 April (Table 3). Males started moulting significantly earlier than females (21 days earlier) (likelihood ratio test, $\chi^2_1=6.63$, $p<0.01$). For three years there were sufficient records to analyse inter-annual variations in the starting date of moult (Table 3), and this is related to rainfall (Figure 6). In 1999/2000 the peak month of rainfall was December (with a smaller peak in March), and males started primary moult on 29 March and females 19 days later. In 2000/01 the peak rainfall month was February, males started moult on 16 April and females 27 days later. In 2003/2004 the peak rainfall months were January – February, males started moult on 25 April and females 13 days later.

The Underhill-Zucchini model was applied to individual primary feathers for adult males in 2000 (Table 4, Figure 7). There were insufficient data in other years or for females for the algorithm to converge. Individual feathers took 11 to 18 days to grow (Table 4). Most apparent overlap in duration of growth of individual primaries was for primaries 1–4 and 9–10. The reduced 10th primary required 11 days to grow, but the SD for this primary was greater than that of the other primaries.

Discussion

Sex differences in body mass and wing length

The biometric data presented in this study are based on a substantially larger sample than hitherto published measurements for *P. r. trothae* (Komen 1990, Table 1), thus

providing a larger range for mass and wing in both sexes. Mean mass for both sexes is within 1 g of Craig's (2004) mean. Mean wing length is greater in Komen's (1990) data by 3.0 mm in males and within 1.0 mm in females.

Seasonal changes in body mass and wing length

Mean mass of both sexes declined after the breeding season and started increasing at the end of moult. This pattern is found in some Ploceidae weavers, but not in others. In Craig's (1978) study of three *Euplectes* species in KwaZulu-Natal, a similar pattern existed; maximum masses were attained at the start of the breeding season by males and at the time of egg-laying by females. Both sexes tended to lose weight during the breeding season, but there was an increase in weight at the time of the post-nuptial moult, before reaching the minimum annual weights during the dry season. This pattern does not apply in Red-headed Weavers *Anaplectes melanotis* where mass does not vary seasonally (Oschadleus 1999). Body mass of Sociable Weavers *Philetairus socius* varied seasonally in different regions without showing clear patterns (Oschadleus 2004).

Wing lengths in male and female Chestnut Weavers decreased extensively as the tips of the outer primaries abraded. Feather wear may be greater in birds living in arid regions than in those in other habitats, due to three environmental factors: thorny vegetation, intense sunlight and exposure to sand (Jenni and Winkler 1994). Herremans (1999) considered that these three factors may explain why Black-chested Prinias *Prinia flavicans* in the Kalahari Desert have a biannual primary moult. Sociable Weavers may have extended duration for primary moult to grow better quality feathers that resist abrasion (Oschadleus 2004). Serra (2001) showed that in Grey Plovers *Pluvialis squatarola* duration of primary moult plays a key role in determining primary quality and hence primary durability, with primary feathers that had been grown fastest showing feather abrasion. In Namibia, Chestnut Weavers build their nests in dense thorny *Acacia* shrubs (Herremans 1997); this may explain why feather abrasion appears to commence during the breeding season.

Timing and duration of primary moult

Komen and Buys (1990) found that adult wing-moult begins after breeding, with males apparently beginning moult earlier than females. The present analysis confirms this. In each of three years, adult males in Namibia started primary moult

two to four weeks earlier than females (Table 3). This is clearly related to the different roles of the sexes in the breeding cycle: males build the nests, copulate with receptive females and then desert the colony soon afterwards, leaving the females to incubate the eggs and rear the young. Thus females postpone the start of moult in order to complete raising the chicks. Primary moult started about a month after the peak rainfall month. This period corresponds with the 28–34 day breeding cycle, thus allowing breeding to fall within the rain period in the study area and primary moult starting as the rains end (Figure 6). Breeding is not restricted to wet years (Komen and Buys 1990), so it would be interesting to compare breeding and moult over more years with greater variation in rainfall.

Ploceidae in semi-arid environments have widely varying primary moult durations, although data have only been analysed rigorously for sedentary Sociable Weavers which have prolonged moult of seven months in the northern Namibian population (*P. s. geminus*) and five to six months in other populations (Oschadleus 2004). Less rigorous moult analyses indicate long moult periods in other arid species weavers. Jones (1978) estimated the duration of primary moult in White-browed Sparrow-weavers *Plocepasser mahali* as six months. Tyler (2001) estimated primary moult duration in Scaly-feathered Finches *Sporopipes squamifrons* as *c.* 7–12 months. The moult durations in Chestnut Weavers in this study (six to seven months) were thus comparable to the moult durations measured in other arid-zone weavers, and longer than those of weavers in the moister eastern and southern parts of southern Africa, where primary moult duration is three to four months (Craig *et al.* 2001).

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Table 1: Mass (g) and wing measurements (mm) by sex of adult Chestnut Weavers in northern Namibia from this study, compared with data from Craig (2004) and Komen (1990). Wing measurements are of birds with new primaries (October – February)

	Males	*Females*
Mass (g)		
Mean	31.2	27.4
Range	23–43	21.1–36
Inter-quartile range (25%)	29.3–33.1	26.3–28.6
Standard deviation	2.6	1.9
n	983	554
Wing (mm)		
Mean	80.7	76.8
Range	70–88.5	69–87
Inter-quartile range (25%)	79–82	75–78
Standard deviation	2.7	2.6
n	528	243
Mass (g), from Craig (2004)		
Mean	32.1	27.8
Range	28–37	25–30
n	39	55
Wing (mm), from Komen (1990)		
Mean	83.7	77.5
Range (from Figure 1)	80–87	74–79
Standard deviation	1.5	1.3
n	42	29

Table 2: Individual primary feather masses (g) of two female and one male Chestnut Weaver specimens from northern Namibia, and the mean relative mass of each primary, used in the calculation of Percentage Feather Mass Grown

Primary	Feather mass (g)						Mean relative feather masses		
	Female 1 right wing	Female 1 left wing	Female 2 right wing	Female 2 left wing	Male 1 right wing	Male 2 left wing	Female	Male	All
1	0.0079	0.0078	0.0085	0.0079	0.0086	0.0083	8.0	7.7	7.8
2	0.0083	0.0082	0.0089	0.0083	0.0090	0.0087	8.4	8.1	8.2
3	0.0088	0.0085	0.0092	0.0090	0.0094	0.0094	8.8	8.6	8.7
4	0.0096	0.0099	0.0102	0.0098	0.0105	0.0102	9.8	9.5	9.6
5	0.0112	0.0117	0.0116	0.0115	0.0121	0.0115	11.4	10.8	11.1
6	0.0121	0.0125	0.0128	0.0126	0.0135	0.0136	12.4	12.4	12.4
7	0.0129	0.0130	0.0130	0.0128	0.0144	0.0143	12.9	13.1	13.0
8	0.0133	0.0136	0.0134	0.0135	0.0152	0.0156	13.4	14.1	13.7
9	0.0142	0.0141	0.0131	0.0134	0.0158	0.0159	13.6	14.5	14.1
10	0.0012	0.0011	0.0014	0.0015	0.0016	0.0014	1.3	1.4	1.3
Total	0.0995	0.1004	0.1021	0.1003	0.1101	0.1089	100.0	100.0	100.0

Table 3: Estimates of the primary moult parameters for adult Chestnut Weavers in northern Namibia, 1999–2004
m=male, f=female

Sex	Year	Mean starting date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Duration (months)	Standard error (days)	Mean completion date	Standard error (days)	n
m	1999–2004	9 Apr	2.9	39.5	1.2	205.8	6.9	3.8	1 Nov	1.8	975
f	1999–2004	30 Apr	3.2	37.5	1.5	189.4	6.3	4.8	5 Nov	2.9	552
m	2000	29 Mar	3.3	37.2	1.2	203	6.8	4.1	18 Oct	2.4	386
m	2001	16 Apr	4.3	37.2	1.2	203	6.8	4.1	5 Nov	2.9	227
m	2004	25 Apr	3.8	37.2	1.2	203	6.8	4.1	14 Nov	5.8	244
f	2000	16 Apr	3.9	35.4	1.5	190.3	6.3	5.3	24 Oct	3.1	223
f	2001	13 May	4.6	35.4	1.5	190.3	6.3	5.3	19 Nov	3.8	133
f	2004	8 May	4.2	35.4	1.5	190.3	6.3	5.3	14 Nov	7.2	101

Table 4: Estimates of the primary moult parameters of individual primary feathers for adult male Chestnut Weavers in northern Namibia in 2000 (n=386)

Primary	Mean starting date	Standard Error (days)	Standard deviation (days)	Standard Error (days)	Duration (days)	Standard Error (days)	Mean completing date	Standard Error (days)
1	28 Apr	3.0	32.1	1.1	14.5	1.2	13 May	2.9
2	8 May	2.8	32.1	1.1	14.5	1.2	22 May	2.9
3	14 May	3.3	23.6	2.5	15.5	2.9	29 May	2.8
4	26 May	2.8	22.2	2.2	12.1	2.4	7 Jun	2.5
5	6 Jun	2.3	18.6	1.6	17.2	2.5	23 Jun	2.2
6	21 Jun	2.2	18.1	1.5	16.3	2.4	7 Jul	2.1
7	7 Jul	2.1	17.5	1.6	13.8	2.2	21 Jul	2.0
8	21 Jul	2.0	17.2	2.1	15.9	2.6	6 Aug	2.3
9	7 Aug	2.5	19.1	2.4	17.9	3.3	25 Aug	3.9
10	18 Aug	3.9	11.4	3.4	11.1	4.2	29 Aug	7.0

Figure 1: Capture sites of adult Chestnut Weavers in the one degree grid cell 19°S 15°E, Namibia, 1999–2004. Solid circles show sites from which biometric and primary moult data were obtained. All the quarter-degree grid cells in Namibia and Botswana in which Chestnut Weavers were recorded during the Southern African Bird Atlas Project are shaded (Herremans 1997)

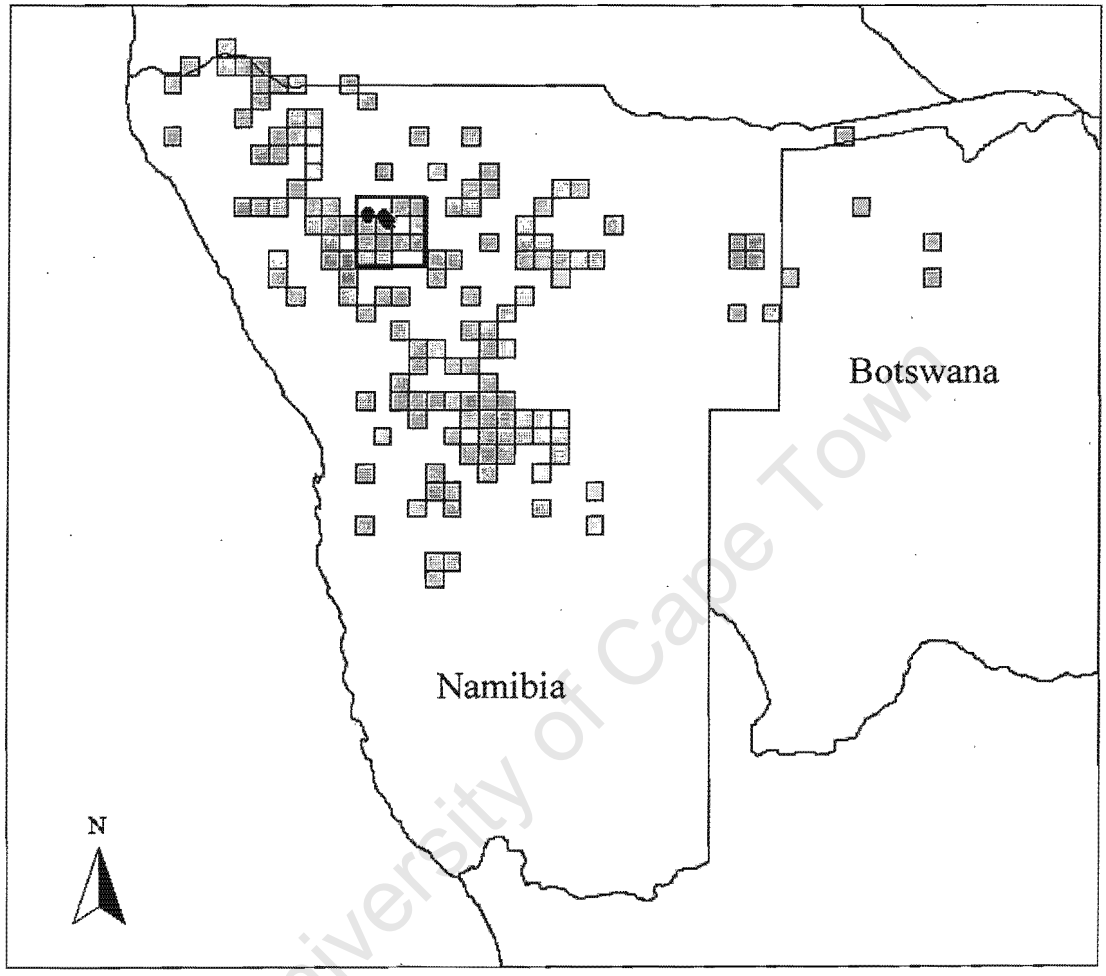


Figure 2: Mean (and SD) body mass (g) of adult Chestnut Weavers by month in northern Namibia, 1999–2004
Sample sizes for males and females respectively are listed under the Month
males, open squares; females, closed squares

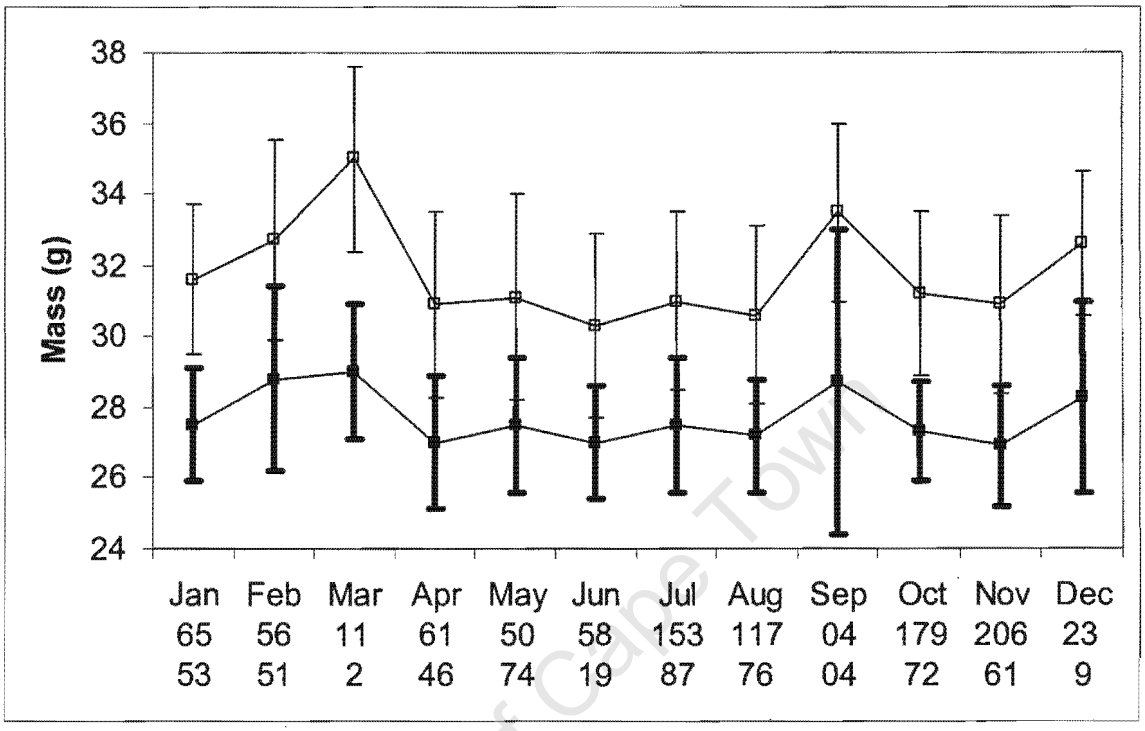


Figure 3: Mean (and SD) wing length (mm) of adult Chestnut Weavers by month in northern Namibia, 1999–2004; wings with primaries 7–9 in moult, are excluded
Sample sizes for males and females respectively are listed under the Month
males, open squares; females, closed squares

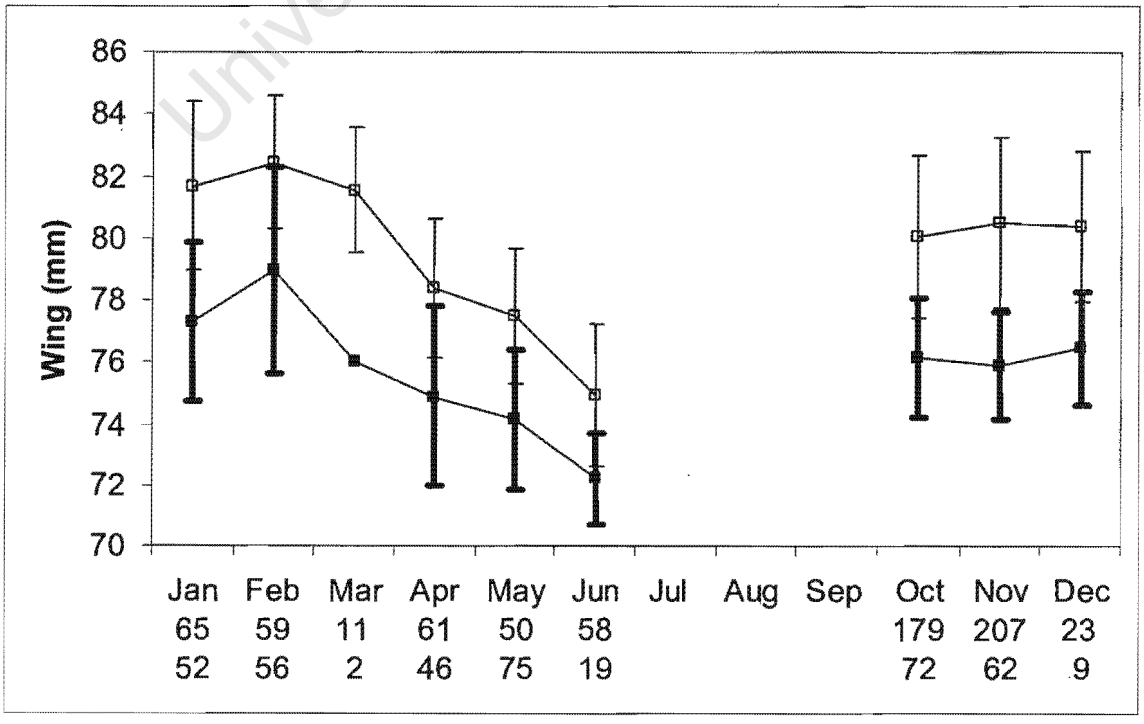


Figure 4: Timing of primary moult for adult male Chestnut Weavers in northern Namibia, 1999–2004; the solid diamonds represent relative feather mass values by date; the solid diagonal line joins the estimated mean start and end dates of moult, while the diagonal dotted lines show the approximate 95% confidence intervals of moult scores on any given date

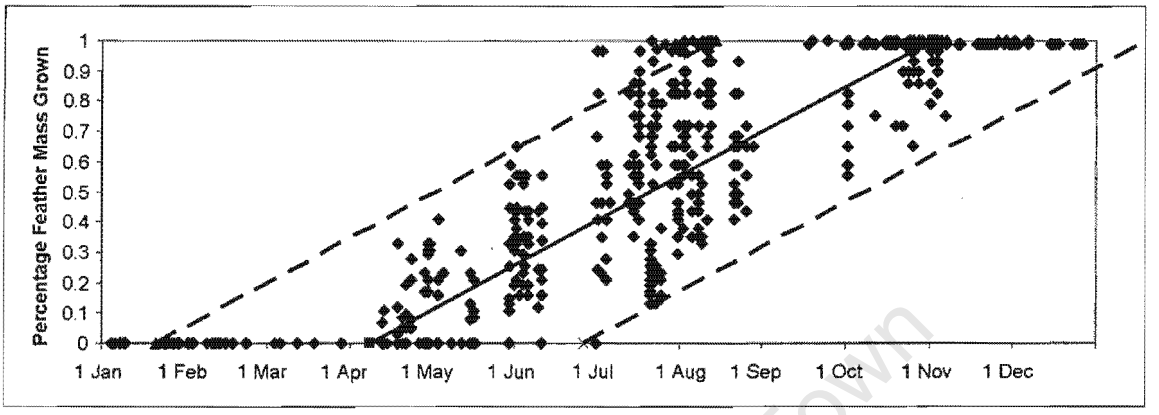


Figure 5: Timing of primary moult for adult female Chestnut Weavers in northern Namibia, 1999–2004; the solid diamonds represent relative feather mass values by date; the solid diagonal line joins the estimated mean start and end dates of moult, while the diagonal dotted lines show the approximate 95% confidence intervals of moult scores on any given date

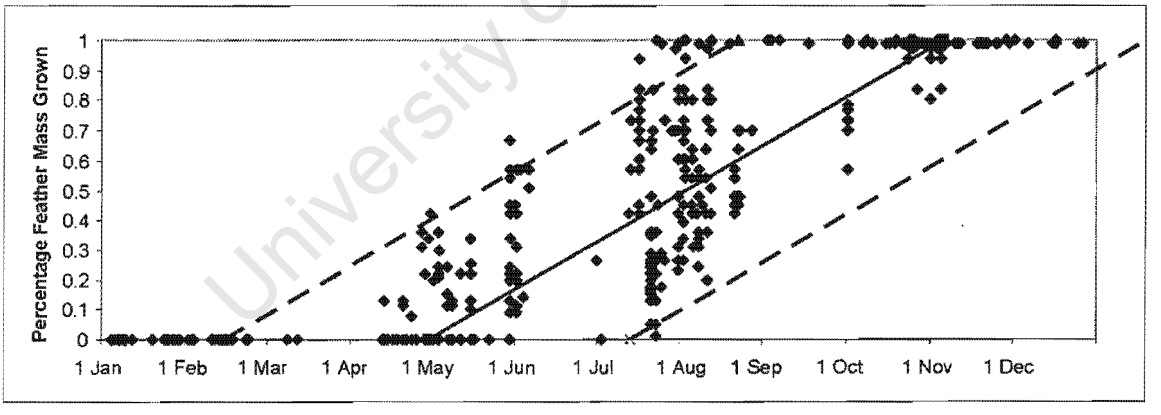


Figure 6: Monthly rainfall at Tandala Ridge, Windpoort Farm, northern Namibia, October 1999 to June 2004. Arrows indicate the mean start of primary moult, with solid arrows for males and dashed arrows for females

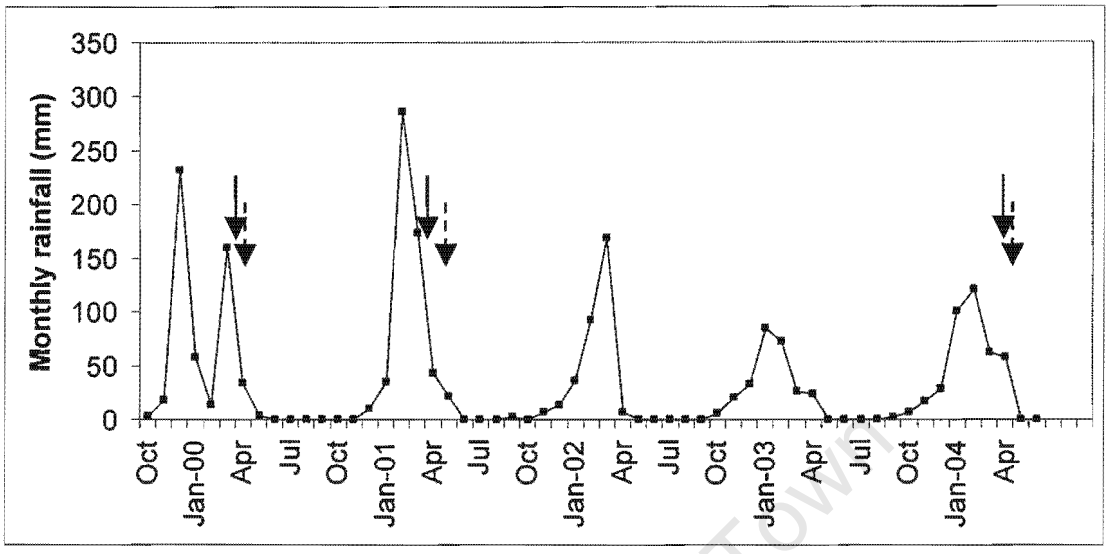
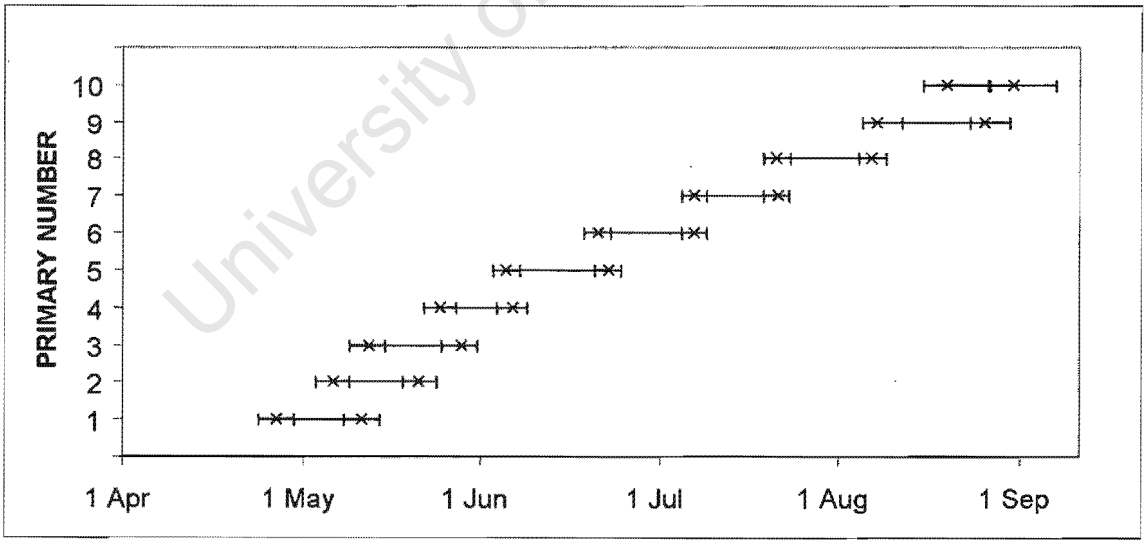


Figure 7: Individual primary growth of adult male Chestnut Weavers in northern Namibia in 2000; crosses indicate the dates of the start and end of moult for each primary feather, and vertical lines indicate standard deviations for 10 primaries; data in Table 4



Chapter 4

The Red-billed Quelea in southern Africa: primary moult and the rainfall migration model

The Red-billed Quelea in southern Africa: primary moult and the rainfall migration model

Abstract

The onset and duration of primary moult were investigated for Red-billed Quelea *Quelea quelea* in southern Africa. Duration of moult was shortest in Namibia (75 days), intermediate in Botswana (83 days) and longest in Gauteng Province, South Africa (101 days). The onset of moult was similar in Namibia and Botswana (21 May and 31 May respectively), but considerably earlier in Gauteng Province (23 April). Completion of primary moult was well synchronized, ending in August in all sub-regions. Production of feather mass was uniform and moult speed was adjusted by the number of primaries growing concurrently – fewer feathers grew simultaneously when moult was faster. Red-billed Queleas are thought to migrate relative to the movement of rain fronts, allowing possible multiple breeding events in one season. Two 'rainfall migration models' were evaluated in the light of the results of the primary moult analyses. Queleas are present throughout their range through the year, and a proportion of the population moves short distances in random directions.

Introduction

The Red-billed Quelea *Quelea quelea*, the most abundant bird species in the world, is an extremely mobile species. Endemic to Africa, it is a major pest of small grain crops and is therefore a major threat to subsistence farmers and of economic importance to commercial farmers (Bruggers and Elliott 1989, Mundy and Jarvis 1989). There are three well-defined populations: *Q. q. quelea* occurs in western Africa from Senegal to Chad; *Q. q. aethiopica* in north-eastern Africa from Sudan to Somalia, north-eastern Zaire, Uganda, Kenya and Tanzania, and *Q. q. lathamii* in southern Africa (Craig 2004). Elliott (1989) estimated the post-breeding population to be 1.5 billion birds.

Although millions of queleas are killed each year in control operations, these birds remain abundant and their range continues to expand (Elliott 1989, Mundy and

Herremans 1997). One of the strategies that makes this species so successful is thought to be itinerant breeding, with individual birds nesting successively at different colonies in optimal conditions during a single breeding season (Bruggers and Elliott 1989). This strategy is known as the 'rainfall-migration model', and was developed by Ward (1971), and elaborated by Jones (1989a,b). At each breeding attempt, the species is monogamous and both parents incubate eggs and feed young. Males leave colonies first, and females frequently have well-developed eggs in their oviducts when they leave their fledglings, which are reared to independence three weeks after hatching (Jones 1989c).

Although the Red-billed Quelea is a particularly well-studied species, remarkably little is known about its moult (Oschadleus 2001); Craig *et al.* (2001) investigated primary moult parameters in quelea in the Eastern Cape and Thompson (1988) compared timing of breeding and moult in Kenya. An understanding of the timing and duration of primary moult is important because it provides insights into a key component of the annual cycle of this successful species. Here, the focus is on the moult of the primary wing feathers, because the main annual moult of many other feather tracts takes place within the period of moult of the primaries. The spatial variation of the primary moult parameters (duration and timing of moult) of the Red-billed Quelea *Q. q. lathamii* were considered at a series of localities in southern Africa. These results were placed in the context of the 'rainfall-migration model', which provides the conventional framework for understanding quelea movements.

Methods

Ringing data were submitted by ringers in the electronic format used by SAFRING (South African Bird Ringing Unit). This includes location, date and primary moult (de Beer *et al.* 2001). Sub-regions were chosen with at least 100 records of birds with growing primaries, with records spread through the moult season, especially at the start and end of primary moult. The following sub-regions were used (Figure 1): one degree grid cell 1915 (= 19°S–20°S, 15°E–16°E) which includes all records from Windpoort Farm (near Etosha Pan) in Namibia; grid 1725 which includes all records from Kasane in extreme northern Botswana; all records from Gauteng Province (Gauteng hereafter),

South Africa (four one-degree grids 2527, 2528, 2627 and 2628 with 55 localities). Results from the Eastern Cape (Craig *et al.* 2001) were compared to records from these sub-regions; a similar data set was reanalyzed using the records from grids 3125, 3225, 3324, 3325 and 3326.

The Red-billed Quelea has nine primary feathers (the 10th primary is vestigial), which are moulted from the innermost primary outwards. The relative masses of each primary (as described in Underhill and Summers 1993) were taken from Craig *et al.* (2001). The Underhill-Zucchini moult model (Underhill and Zucchini 1988), developed to estimate the start and duration of primary moult, was applied to the data sets. The data were considered to be of 'type 2' (Underhill and Zucchini 1988), because full moult scores were recorded for each bird and all birds were considered available for sampling throughout the moult period. The parameters of primary moult were estimated using the transformations recommended by Summers *et al.* (1980, 1983), designed to reduce the bias introduced by the fact that the individual feathers are of different masses. The moult index used was percentage feather mass grown (PFMG), calculated from the moult score for the individual feathers according to the method of Underhill and Summers (1993). In addition, this analysis was undertaken to estimate the parameters of moult of each individual primary (Underhill 2003, Underhill *et al.* in press).

Results

2881 ringing records and five recapture records were obtained for adult Red-billed Queleas in the target grid cells in Namibia, Botswana and Gauteng between March 1999 and December 2004; an additional 2970 ringing and 75 recapture records between March 1995 and January 2004 are available for the Eastern Cape, including the records published in Craig *et al.* (2001). Birds were considered to be in arrested moult if both new and old primary feathers were present, and there were no growing feathers. The percentages of birds with arrested moult varied widely: in Botswana, it was 6.1%; in Namibia 0.2%; in Gauteng 1.5%; and 0.4% in the Eastern Cape. These birds were excluded from the primary moult analysis. Of birds in moult, the number of simultaneously growing primary feathers per individual varied by sub-region. In

Namibia, most birds moulted one primary at a time, but about 7% moulted two; in Botswana the proportion moulting two primaries simultaneously increased to 19%; in Gauteng and the Eastern Cape, up to four primaries were moulted simultaneously, with more than half of the birds moulting two primaries (Table 1).

Capture of moulting birds was distributed fairly evenly over the moulting season (Figure 2); this improves the reliability of the moult estimates. In Namibia, duration of moult in adults was estimated to be 75 days (2.5 months) and the mean starting date was 21 May. In Botswana duration of moult in adults was estimated to be 83 days (2.8 months) and the mean starting date was 31 May. In Gauteng duration of moult in adults was estimated to be 101 days (3.4 months) and the mean starting date was 23 April (Table 2).

The Underhill-Zucchini model was applied to individual primary feathers for adult birds (Table 3, Figure 3). There was a high degree of overlap between sub-regions in duration of growth of individual primaries. In Gauteng the individual feathers took between 17 and 36 days to grow, in the Eastern Cape 18 to 29 days, in Botswana 10 to 18 days, and in Namibia 6 to 15 days. In the latter two sub-regions, however, duration of moult could not be calculated for all individual primaries (Table 3).

Using the information in Table 3 for quelea in Gauteng and the Eastern Cape, and simplistically assuming that each feather grows uniformly, the proportion of the total primary mass produced each day was calculated (Figure 4). In Gauteng this varied between 0.57% and 1.46% (apart from one exceptional day when primaries 8 to 10 were all estimated to be growing): the rate was lowest (at 0.57%) when primaries 1 and 2 were growing, and peaked at 1.46% over a nine-day period, when primaries 9 and 10 were growing. In the Eastern Cape, the birds initially displayed a slightly higher relative growth rate, but this then stabilized between 0.51% and 1.04%.

Discussion

Comparison of moult parameters between sub-regions

Primary moult commenced earliest in the Eastern Cape, 2–3 weeks later in Gauteng, and last (6–8 weeks later) in northern Botswana and northern Namibia. This trend is

consistent with the general pattern for southern African passerines, namely that primary moult commences after the completion of breeding, and usually takes place in autumn and winter. The length of the delay across southern Africa is similar to the average delay in the onset of the wet seasons across southern Africa between the south-east and the north-west (Allan *et al.* 1997).

The pattern of duration of moult of individual feathers was unexpected, and varied widely in the different sub-regions (Table 3). In Gauteng the outer primary, which is the heaviest and accounts for 14.8% of total primary feather mass (Craig *et al.* 2001), was the fastest to grow (17 days). The four small inner primaries, accounting for 8.0% to 9.9% of total feather mass, took up to twice as long to grow (25 to 36 days). However, while the inner primaries were being moulted, three or four primaries were often growing simultaneously. While the outer primaries were being moulted, one or two primaries were growing (Table 1, Figure 3).

This moult strategy results in fairly uniform production of feather keratins (Figure 4). A shorter moult duration (i.e. fast moult) was achieved by growing fewer feathers concurrently but growing them rapidly. The outermost primary grows five times faster in Namibia (6 days, Table 3) than in the Eastern Cape (29 days). Zenatello *et al.* (2002) showed that Black Terns *Chlidonias niger* can either moult many primaries at a slow speed, or less primaries at a faster speed. These results are contrary to those found for Common Starlings *Sturnus vulgaris*, which grew more feathers concurrently to achieve shorter moult periods (Dawson 2004). Serra (2002) demonstrated that feather quality was related to moult speed in Grey Plovers *Pluvialis squatarola*.

It was striking that the timing of the completion of moult in the four sub-regions was more synchronized than the commencement of moult. In three of the four sub-regions, the mean completion dates lay between 2 and 8 August, and the mean completion date in northern Botswana was two weeks later (Table 2). This synchronization of completion dates was possible because the duration of Red-billed Quelea primary moult was shortest in Namibia at 75 days, with progressively longer mean durations for birds towards the south-east, with an estimated duration of 124 days in the Eastern Cape (Figure 1, Table 2). In each sub-region, most individual birds would have completed moult by the end of September. Throughout the breeding range of the

Red-billed Quelea in the summer rainfall region of southern Africa, the period September to November is the longest time since the last production of natural grass seeds, and the period when food is least abundant. It is therefore probably the period during which moult should not be undertaken.

The most likely reason for the variation in moult duration is related to the movements of the species. Birds migrating to Botswana and Namibia breed and then start moult, but consequently have less time to complete their moult. A consequence is that birds in Namibia may grow feathers of a lower quality than in the eastern parts of southern Africa; this needs to be investigated further.

Moult in the annual cycle and the rainfall-migration model

Ward (1971) considered that Red-billed Queleas carry out migrations which are related to the progress of rain fronts and consequent availability of food. In southern Africa, Jones (1989a, b) applied this hypothesis to the movements of Red-billed Quelea, and proposed a rainfall-migration model for the species in this region. This model is based on a simplified pattern of the initiation of the wet season across the summer rainfall zone of southern Africa and its impact on the germination of natural grass seed. Along a south-east to north-west transect from KwaZulu-Natal to northern Namibia, the onset of the heavy rains that trigger seed germination is progressively later (Allan *et al.* 1997, Figure 15). Optimal conditions for breeding, namely the availability of fresh grass seed and insects, occur six to eight weeks after the start of the heavy rains. According to this model, quelea undertake a long pre-breeding migration across the rain fronts towards the south-east in November, arrive in areas with good breeding conditions about six-eight weeks after the rains, and start breeding. The breeding cycle takes about seven weeks (nest construction and egg laying overlap and are completed in six days; incubation lasts 9–10 days; the nestling period takes 11–13 days; chicks fledge at age 16 days, commence self-feeding at 19 days, and are independent fledglings within a day or two after this) (Jones 1989c). The emergence of fresh grass seeds progresses steadily towards the north-west. Adults desert breeding colonies as soon as fledglings are independent, move north-west to find places where the heavy rains started six to eight weeks previously, and breed again in good conditions, probably several hundred kilometres north-west of the previous

breeding event. In terms of this model, Red-billed Queleas are described as itinerant breeders, and the north-west movement to successive breeding colonies is known as the breeding migration (Ward 1971, Jones 1989b). The model envisages regular north-west to south-east migrations between South Africa, Botswana and Namibia, over distances in excess of 1000 km (Ward 1971, Jones 1989b).

Because of the enormous variability in the pattern of rainfall events in southern Africa between years, this model is an over-simplification, but the underlying principle of itinerant breeding is likely to be correct (Jarvis 1989). Breeding of the same bird at more than one locality in a single breeding season has not yet been demonstrated in southern Africa, but has been shown to occur in Ethiopia (Jaeger *et al.* 1986).

Jarvis (1989) pointed out that a modified version of the rainfall migration model was more likely to be appropriate; he suggested that the pattern of movement would be on a much shorter scale than that envisaged by Ward (1971) and Jones (1989a, b). The early-summer rainfall pattern in southern Africa entails scattered thunder storms resulting in patchy rain, and Jarvis (1989) envisaged queleas moving between the suitable habitat patches these rains would generate. At the start of the rainy season, the birds would need to locate dry areas where grass seeds had not yet germinated, until such time as they could locate breeding sites. The latter would be places where heavy rain had fallen six to eight weeks earlier, and where green seeds and insects were abundant. Jarvis (1989) suggested that most movements would not be on the classic north-west to south-east axis, but in random directions and over relatively short distances.

The rainfall migration model of Ward (1971) and Jones (1989) was never presented as a partial migration model and it assumed that the overwhelming majority of queleas moved along the north-west to south-east axis. The broad-brush seasonal analysis of the data in the Southern African Bird Atlas Project (Mundy and Herremans 1997) did not support this idea. On a finer scale, Allan *et al.* (1995) used the same data, and split the range of the quelea in southern Africa into 12 areas and found that, at this level, 'quelea are present throughout their range virtually throughout the year'. They found that reporting rates for queleas showed little seasonal variation, apart from the South African lowveld (northern KwaZulu-Natal and the Kruger National Park) where there were higher reporting rates during the summer breeding season, indicating influxes of birds. A

similar pattern of continuous presence was observed in southern Mozambique (Parker 1999), whereas in central Mozambique, unexpectedly, reporting rates were highest in midwinter (Parker 2005). A century ago, Haagner (1905) noted that some quelea were resident in Gauteng while other individuals passed through on migration. These results lend support to Jarvis' (1989) short-distance rainfall migration model. The ringing data on which this paper is based also demonstrated that quelea were present in each of the study areas throughout the year, not just in the breeding season or during the moult period. The small number of recaptures obtained was consistent with the magnitude of the quelea population.

It is impossible to interpret the SAFRING ring recovery data in terms of the long-distance rainfall migration model. Oschadleus (2000a) plotted patterns of recoveries on a monthly basis; most movements were not along the north-west to south-east axis predicted by the rainfall migration model. The overwhelming majority of the 510 recoveries were over distances less than 100 km and were in all directions from the site of ringing. The ring recovery data thus also support the Jarvis (1989) short-distance rain migration model.

Agricultural activities have undoubtedly modified the movement pattern of queleas. Small-grain farming and the development of feed lots for livestock provide food at times when it would otherwise be scarce, so that birds do not need to be as nomadic as in the past (Mundy and Herremans 1997, Whittington-Jones *et al.* 2001). Quelea are obligate drinkers and the development of networks of dams (both small farm dams and large reservoirs) in areas with no open water has enabled queleas to exploit areas in which they could not otherwise have survived. Overgrazing, and consequent bush encroachment in previously treeless areas, have also provided sites for breeding colonies in areas that were previously unsuitable (Jones 1989b).

The geographical pattern of breeding seasonality predicted by the long-distance rainfall migration model is weakly supported by a trend in the timing of breeding; in South Africa it is December to April, in Botswana December to April, and in Namibia January to April (Craig 2004). The later start to breeding in Namibia is more parsimoniously explained in terms of late onset of rains than by the arrival of birds from the south-east on migration.

The two-month delay in the onset of heavy rains in northern Namibia relative to south-eastern South Africa, coincides closely with the difference in the data of the commencement of moult across the region (Table 2). Our results therefore suggest that primary moult takes place immediately after the completion of breeding.

If the long-distance rainfall migration model were correct, movements across southern Africa would generate extensive mixing, and all birds would belong to a single meta-population. One would therefore predict that, apart from the timing of the start of moult which is related to breeding seasonality, moult parameters would be similar throughout the region. This is not the case. The observed regional differences in duration of moult are large, between 75 days and 124 days (Table 2), as are the strategies whereby individual primaries are moulted (Figure 3). The proportion of birds moulting only one primary at a time varied from 93% Namibia to 22% in the Eastern Cape (Table 1). It seems unlikely that regional differences of this magnitude could exist within a single meta-population that is continuously being mixed up by long-distance migration, and more likely to be explained by regional adaptations along environmental clines. Thus the results of this moult study also lend support to the Jarvis (1989) short-distance rain migration model.

Strengths, limitations and extensions of this study

This study benefited from the fact that the moult parameters were estimated at all localities using the same fieldwork protocol; this is a by-product of the series of SAFRING training courses conducted twice-yearly since March 2000 (Oschadleus 2000b). It also benefited from the use of a single statistical model to undertake the statistical analyses of the primary moult data; this has also been highlighted by Serra (2002), who demonstrated the importance of using uniform methods in making fine-scale comparisons of the timing and duration between sites.

The Underhill-Zucchini moult model assumes that the sample of moulting birds is a representative sample of a population of birds. If nomadic behaviour during moult generates a passage of birds through the study site in such a way that populations passing through have different moult parameters, then the data collected at the site would not be

representative of any real population. However, the ring-recovery data provide no evidence that this pattern of movement occurred.

At each study site, data for several years were combined because sample sizes in any single year were small. This is not ideal, because there may be inter-year differences in moult parameters. At best, the consequence of this is that the moult appears less synchronized than it actually is in an individual year. At worst, a large sample of birds from a single year in which moult is particularly early or late can bias the results. This latter scenario is unlikely, because the contributions of data from single days were generally small. The results from each of our study areas are likely to be representative of the average moult parameters at the site.

This analysis has revealed geographical patterns in the timing and duration of primary moult across southern Africa. Data from a selection of sites across the subcontinent would confirm the geographical pattern of timing of moult, and the pattern of duration, which were not anticipated. Further studies of the primary moult of the Red-billed Quelea should concentrate on an understanding of inter-year variation at a study site; this requires sampling at regular intervals throughout the moult period of the population at the selected site over several years.

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Table 1: The number of observations of each primary feather of adult Red-billed Queleas in active moult in different regions of southern Africa, and the percentages of primaries actively moulting while each primary was in moult. The averages are unweighted

(a) Namibia, grid cell 1915

Primary	No. in moult	1 active	2 active
1	1	100.0	0.0
2	3	100.0	0.0
3	9	77.8	22.2
4	9	77.8	22.2
5	13	92.3	7.7
6	23	95.7	4.3
7	32	96.9	3.1
8	34	97.1	2.9
9	18	100.0	0.0
Average		93	7

(b) Botswana, grid cell 1725

Primary	No. in moult	1 active	2 active	3 active
1	2	50.0	50.0	0.0
2	6	33.3	33.3	33.3
3	18	55.6	27.8	16.7
4	29	62.1	27.6	10.3
5	22	77.3	18.2	4.5
6	39	100.0	0.0	0.0
7	37	100.0	0.0	0.0
8	25	96.0	4.0	0.0
9	8	87.5	12.5	0.0
Average		74	19	7

(c) Gauteng Province

Primary	No. in moult	1 active	2 active	3 active	4 active
1	25	8.0	60.0	24.0	8.0
2	44	13.6	47.7	31.8	6.8
3	46	23.9	34.8	34.8	6.5
4	55	30.9	43.6	20.0	5.5
5	44	29.5	59.1	9.1	2.3
6	45	35.6	57.8	6.7	0.0
7	43	25.6	67.4	7.0	0.0
8	35	25.7	68.6	5.7	0.0
9	27	63.0	33.3	3.7	0.0
Average		28	53	16	3

(d) Eastern Cape

Primary	No. in moult	1 active	2 active	3 active	4 active
1	116	14.7	44.0	34.5	6.9
2	141	3.5	51.1	39.7	5.7
3	170	9.4	40.0	45.9	4.7
4	177	9.0	61.0	25.4	4.5
5	220	19.1	67.3	13.6	0.0
6	244	25.4	70.9	3.7	0.0
7	209	27.3	69.9	2.9	0.0
8	205	27.8	69.8	2.4	0.0
9	236	63.1	35.2	1.7	0.0
Average		22	57	19	2

Table 2: Estimates of the primary moult parameters for adult Red-billed Queleas in southern Africa, 1999–2004; * Eastern Cape data from Craig *et al.* (2001)

Region	Mean starting date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Standard error (days)	Mean completion date	Standard error (days)	n
Namibia	21 May	4.3	37.4	1.9	74.6	4.8	3 Aug	2.7	1163
Botswana	31 May	3.6	35.1	1.8	82.5	4.5	21 Aug	2.6	543
Gauteng	23 Apr	2.6	32.7	1.2	100.9	3.6	2 Aug	2.4	1105
E Cape *	6 Apr	2	36.5	0.8	124	3	8 Aug	1.4	3077

Table 3: Estimates of the primary moult parameters of individual primary feathers for adult Red-billed Queleas in different regions of southern Africa; primary 10 is minute and is omitted

(a) Namibia (n=1163)

Primary	Mean starting date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Standard error (days)	Mean completing date	Standard error (days)
3	2 Jun	3.8	28.1	2.6	7.2	2.3	9 Jun	3.5
4	6 Jun	3.9	30.8	2.9	6.4	2.0	13 Jun	3.6
5	12 Jun	3.9	32.1	3.0	7.8	2.1	20 Jun	3.5
6	18 Jun	3.8	34.9	3.0	12.1	2.5	30 Jun	3.3
7	28 Jun	3.8	39.5	2.9	15.0	2.6	13 Jul	3.3
8	11 Jul	3.5	42.0	2.6	14.2	2.3	25 Jul	3.2
9	24 Jul	3.1	40.1	2.6	6.1	1.5	30 Jul	3.0

(b) Botswana (n=543)

Primary	Mean starting date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Standard error (days)	Mean completing date	Standard error (days)
3	3 Jun	3.1	26.7	2.1	12.0	2.6	15 Jun	3.0
4	10 Jun	3.3	30.9	2.1	18.3	3.0	28 Jun	3.0
5	23 Jun	3.3	34.6	2.5	12.0	2.4	5 Jul	3.1
6	6 Jul	3.3	35.4	2.5	17.5	2.6	24 Jul	2.9
7	22 Jul	3.2	38.8	2.9	14.8	2.4	6 Aug	2.9
8	5 Aug	3.0	39.3	3.2	9.6	1.9	15 Aug	2.9

(c) Gauteng Province (n=1105)

Primary	Mean starting date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Standard error (days)	Mean completing date	Standard error (days)
1	19 Apr	3.5	42.3	2.5	24.9	3.3	14 May	3.2
2	19 Apr	3.4	39.4	2.3	35.0	3.5	24 May	3.0
3	29 Apr	3.3	37.5	2.1	34.6	3.4	2 Jun	2.9
4	10 May	3.1	36.4	1.9	36.2	3.3	15 Jun	2.8
5	26 May	3.2	38.8	2.0	29.6	3.1	25 Jun	2.9
6	8 Jun	3.1	37.0	1.9	28.6	3.0	7 Jul	2.8
7	22 Jun	3.0	34.7	1.8	26.7	2.9	18 Jul	2.6
8	5 Jul	2.9	31.9	1.7	22.9	2.7	27 Jul	2.5
9	18 Jul	2.9	32.8	1.8	17.2	2.4	4 Aug	2.5

(d) Eastern Cape (n=2738)

Primary	Mean starting date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Standard error (days)	Mean completing date	Standard error (days)
1	9 Apr	2.3	30.7	1.4	17.8	1.9	27 Apr	3.2
2	12 Apr	2.3	31.3	1.4	20.0	1.9	2 May	3.0
3	17 Apr	2.2	32.7	1.5	24.6	2.0	12 May	2.9
4	27 Apr	2.1	34.1	1.6	25.1	1.9	22 May	2.8
5	10 May	2.0	35.6	1.6	26.8	1.9	5 Jun	2.9
6	26 May	1.7	34.0	1.6	22.9	1.7	18 Jun	2.8
7	11 Jun	1.8	40.4	1.5	23.4	1.7	4 Jul	2.6
8	27 Jun	1.8	40.1	1.4	25.4	1.7	22 Jul	2.5
9	10 Jul	1.7	39.3	1.3	29.2	1.7	8 Aug	2.5

Figure 1: Capture sites of adult Red-billed Queleas in selected one degree grid cells, 1995–2004. Black dots in the grid cells show sites from which primary moult data were obtained; the three Eastern Cape grids show the ringing sites that Craig *et al.* (2001) used. All the quarter-degree grid cells in southern Africa in which Red-billed Queleas were recorded during the Southern African Bird Atlas Project are shaded (Mundy and Herremans 1997)

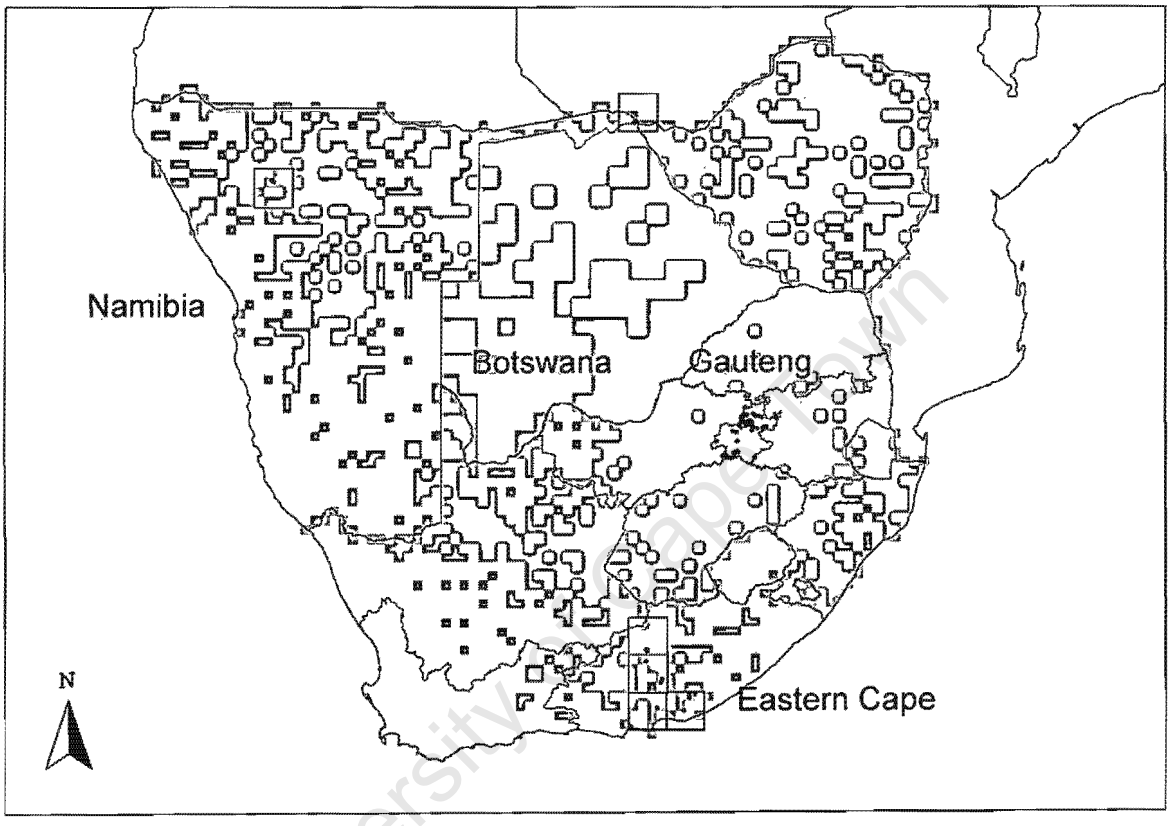
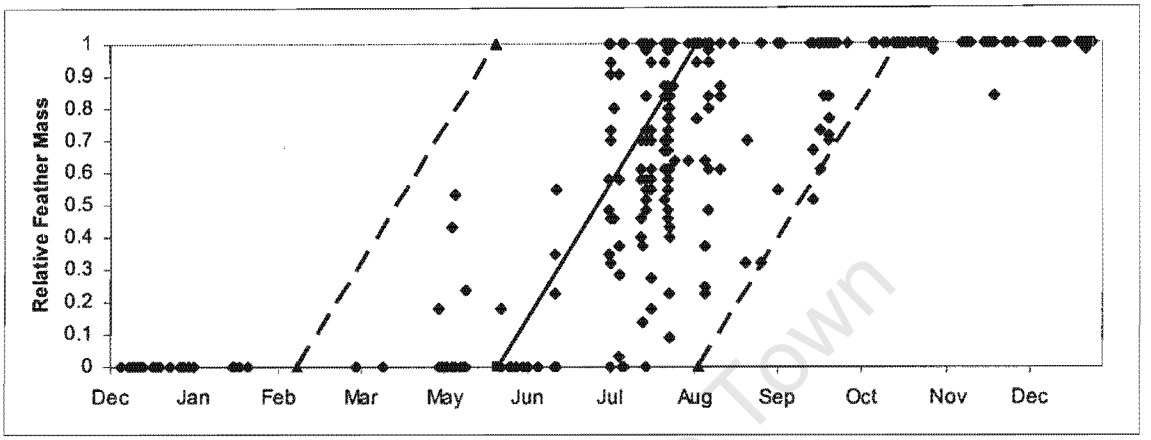
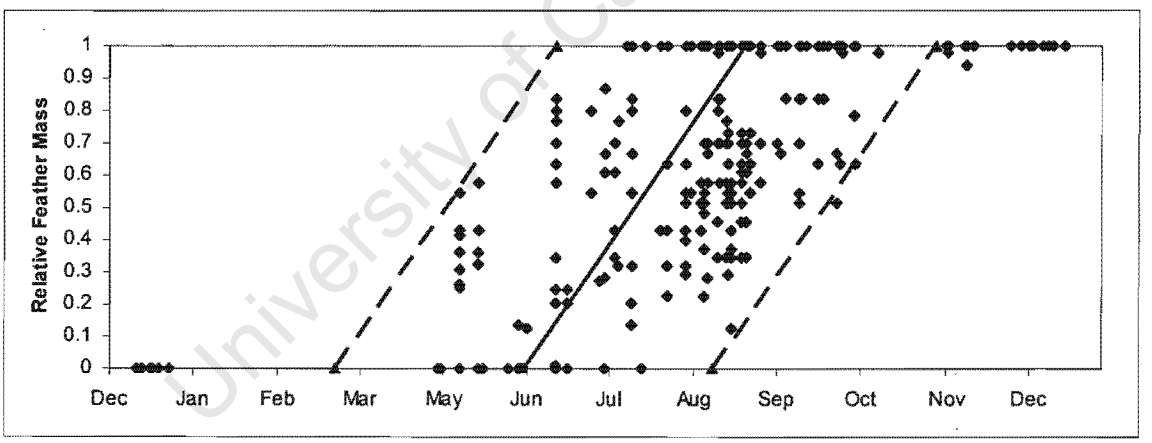


Figure 2: Timing of primary moult for adult Red-billed Queleas in three regions in southern Africa; the solid diamonds represent relative feather mass values by date; the solid diagonal line joins the estimated mean start and end dates of moult, while the diagonal dotted lines show the approximate 95% confidence intervals of moult scores on any given date

(a) Grid cell 1915, Namibia



(b) Grid cell 1725, Botswana



(c) Gauteng Province, South Africa

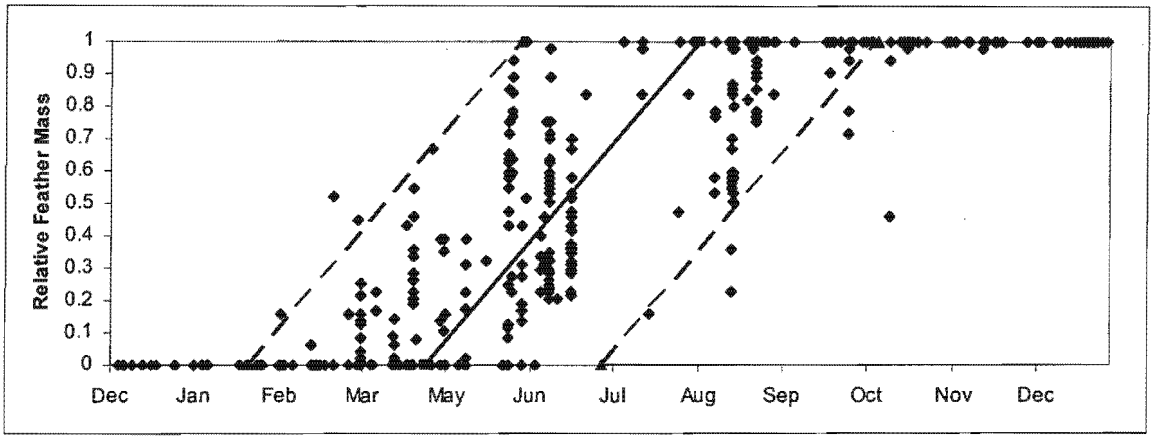
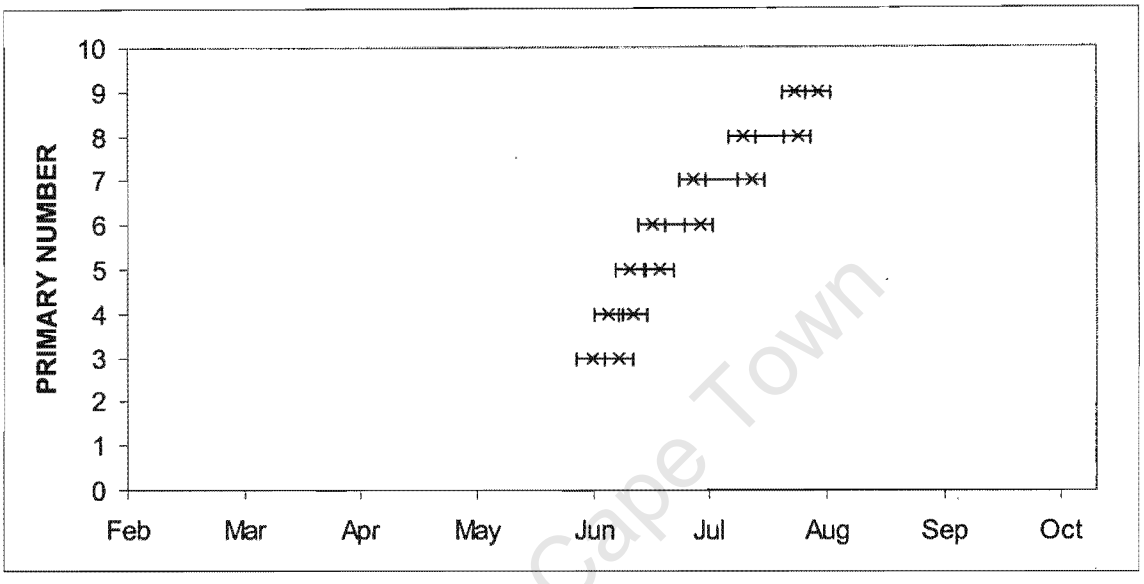
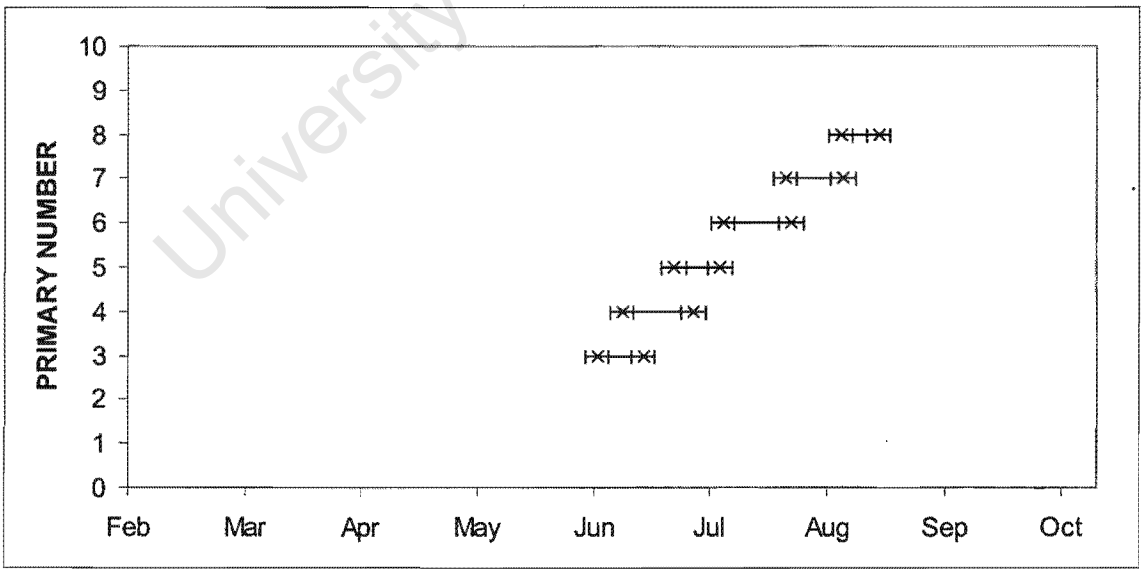


Figure 3: Individual primary growth of adult Red-billed Queleas in different regions in southern Africa; crosses indicate the dates of the start and end of moult for each primary feather, and distances between pairs of vertical lines indicate standard errors for nine primaries; data in Table 3

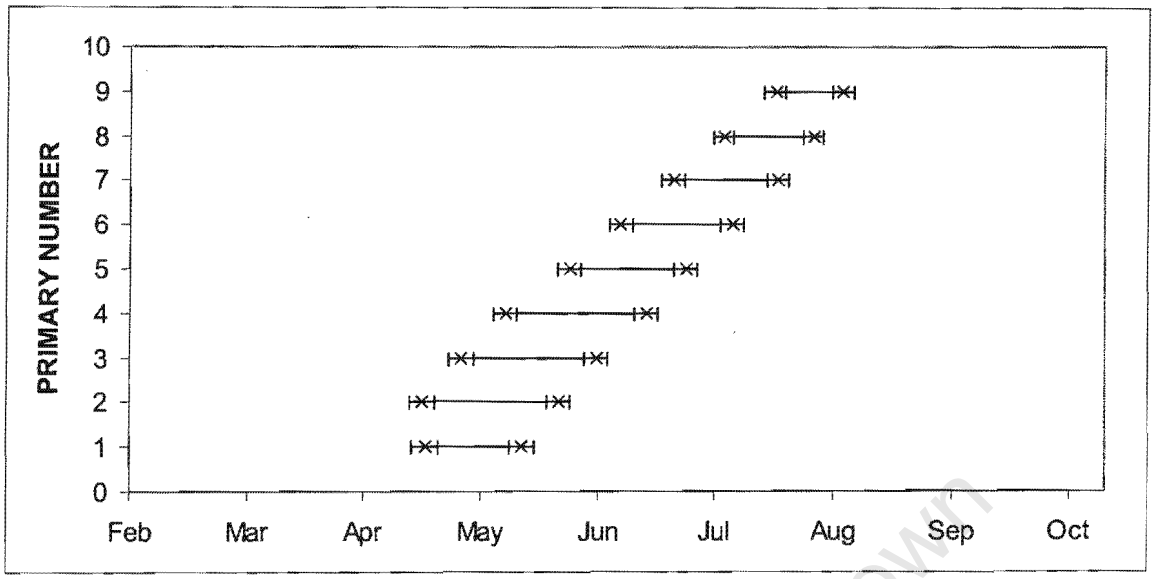
(a) Individual primary growth of adult Red-billed Queleas in Namibia



(b) Individual primary growth of adult Red-billed Queleas in Botswana



(c) Individual primary growth of adult Red-billed Queleas in Gauteng Province



(d) Individual primary growth of adult Red-billed Queleas in the Eastern Cape

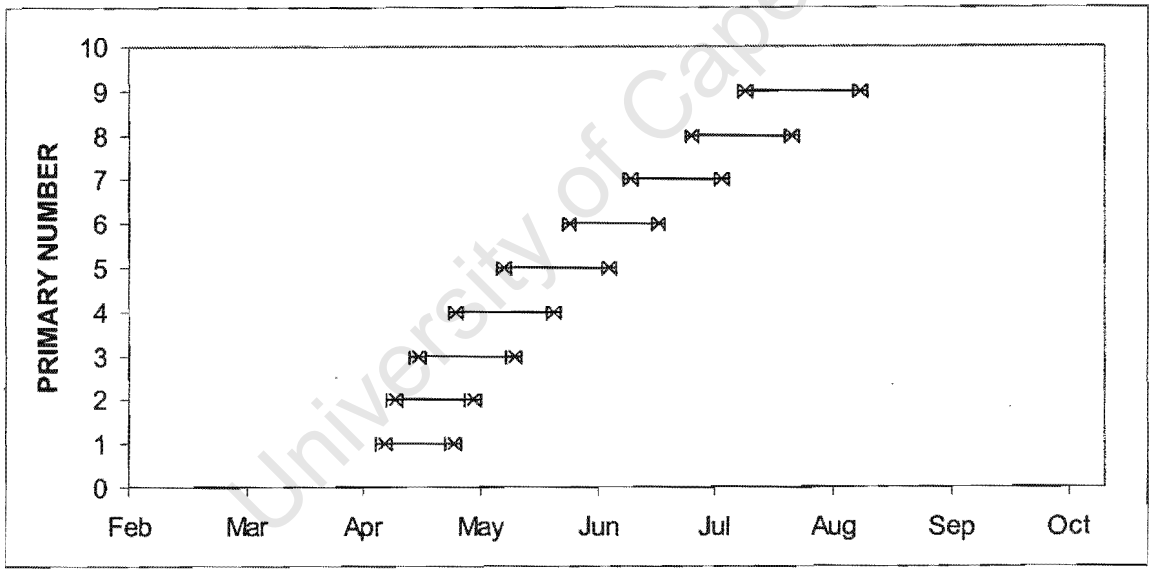
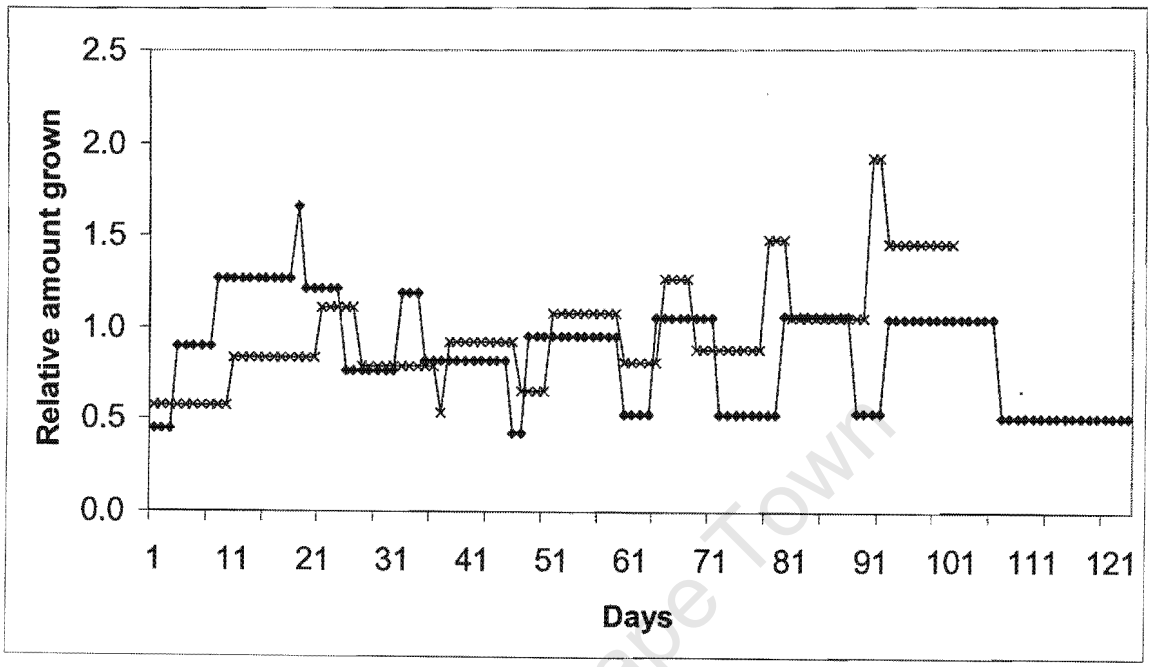


Figure 4: Model of the relative amount of the total primary mass produced each day for adult Red-billed Queleas in two regions in South Africa, the Gauteng Province (crosses) and the Eastern Cape (closed diamonds)



Chapter 5

Geographic variation in breeding seasonality and primary moult parameters in Cape Weavers, Southern Masked Weavers and Southern Red Bishops in South Africa

Geographic variation in breeding seasonality and primary moult parameters in Cape Weavers, Southern Masked Weavers and Southern Red Bishops in South Africa

Abstract

The Southern Masked Weaver *Ploceus velatus* expanded its range into the south-western part of the Western Cape, and here it has advanced its peak breeding and moult onset by one month relative to other areas, but is still a month behind that of the Cape Weaver *P. capensis*. Peak breeding in the Southern Red Bishop *Euplectes orix* is the same as that of the two *Ploceus* species in KwaZulu-Natal, and retarded by one or two months in the other regions. Southern Masked Weavers use trees and reeds equally early in different parts of South Africa. Variation in start and end of breeding depends largely on rainfall. In the three ploceids, primary moult started in the same month that the last eggs are laid. For the Cape Weaver moult started progressively later along the coast from the Western Cape to KwaZulu-Natal, and duration of primary moult varied from 3.3 months to 4.1 months. In Southern Masked Weavers moult started between 27 December and 22 March, while duration of moult was 2.2 to 2.8 months. In Southern Red Bishops moult started early in the Western Cape (13 December), and much later in the other regions. Duration of moult varied from 2.4 to 3.1 months.

Introduction

The Cape Weaver *Ploceus capensis,* Southern Masked Weaver *P. velatus* and Southern Red Bishop *Euplectes orix* are three common ploceids found in South Africa. They are polygynous, colonial, seed-eating ploceids (Fry and Keith 2004). The distributions of the three species span regions with contrasting rainfall patterns: the winter rainfall region of the Western Cape, with a typical Mediterranean climate, the south coast region with rain throughout the year, and the summer rainfall region over the remainder of South Africa (Allan *et al.* 1997). Within South Africa, the strongest climate gradients are east-west (Allan *et al.* 1997). The winter-rainfall region of the Western Cape is on the same latitude band (33°–35°S) as the summer-

rainfall region of the Eastern Cape. Within the summer rainfall region (24°–30°S), there is a gradient from subtropical coastal forest on the east coast to desert on the west coast. The Western Cape largely contains the fynbos biome, while Gauteng and KwaZulu-Natal are mainly in savanna and grassland biomes. The Eastern Cape is a transition area with a mixture of biomes.

The extent of local movements by birds determines the environmental conditions to which they are exposed during a year. None of the three ploceids studied here are long-distance migrants. Based on ring recoveries, the median distance moved by Cape Weavers and by Southern Masked Weavers was 4 km and 1 km, respectively (Oatley and Underhill 2001). At all percentiles, the dispersal distances of Cape Weavers were about three times as great as those of Southern Masked Weavers (Oatley and Underhill 2001). The Southern Masked Weaver, inhabiting arid areas with unpredictable rainfall, should be the species most compelled to move about to seek patchy food resources. Herremans (1994) presented evidence that the Southern Masked Weaver is a partial migrant in south-eastern Botswana, based on the emigration of juveniles and sometimes also females during the dry winter season. Southern Red Bishops do not move great distances. 79% of recoveries were at the original capture site and 20% were within 20 km from the original capture site (n = 1520); the greatest distance between ringing and recovery site reported was 112 km (Friedl 2004). In the non-breeding season Southern Red Bishops are nomadic, frequenting grasslands and agricultural lands in large flocks, often in association with other *Euplectes* species (Craig 1980).

The Southern Masked Weaver is a relatively new arrival in the Western Cape, having expanded its range into this region in the last 60 years. Brooke (1985) reviewed the literature concerning the early published records of this bird in the Western Cape, while MacDonald (1990) investigated its expansion westwards through the Karoo. Oschadleus *et al.* (2000) provide evidence of an earlier range expansion based on the Nest Record Collection of BirdLife South with records from 1921 and 1925.

Annual variation in breeding seasonality and in starting date of moult and duration of moult in relation to climatic and environmental conditions have not been well studied in African birds (Craig 1983). In broad terms, breeding by the three ploceids considered in this paper is in the summer months and is known to be earlier in the winter rainfall region compared to the summer rainfall region (Oschadleus *et al.*

2000, Craig *et al.* 2001). In the Western Cape adult wing-moult is from October to March in Cape Weavers, November to April in Southern Red Bishops (Craig *et al.* 2001), and January to March in Southern Masked Weavers (Oschadleus *et al.* 2000).

The aims of this paper are to investigate variation in breeding seasonality and timing and duration of primary moult in three common ploceids in South Africa. In particular these differences are investigated in different climate zones which lie on the same latitude, thus factoring out the effect of day-length (see Oschadleus *et al.* 2001). Craig *et al.* (2001) suggested later breeding by Southern Red Bishops may be related to nesting sites so nest sites are analysed. The timing of moult of long-established species in the winter rainfall region (Cape Weaver and Southern Red Bishop, Layard 1867) is compared with the newly established Southern Masked Weaver. Finally, timing of breeding is related to timing of moult in all three species.

Methods

Breeding seasonality data were obtained from the BirdLife South Africa Nest Record Card Scheme (NRC) (RP Prŷs-Jones and I Newton unpublished data; Underhill *et al.* 1991) and by adding my own unpublished records of breeding for Southern Masked Weavers in Dundee, KwaZulu-Natal. Prŷs-Jones and Newton (unpublished data) estimated the month of laying of the first egg for each record. They then summarised breeding seasonality for all birds in South Africa by presenting monthly totals of clutches laid per species per region. One of the regions they used was the former Transvaal province: this region incorporates the current Gauteng Province, from where most of the records originate anyway. To compare breeding seasonality of weavers, the tabulated data of Prŷs-Jones and Newton were used to estimate the median and the 5th and 95th percentiles for each species and region. The median was calculated by finding the cumulative monthly sums of the percentage of nest records. The median month was the month in which the cumulative sum first exceeded 50%. The values of the sums of the previous and successive months were used to assign a relative distance into the month. For example, if there were 47% of cumulative records by the end of October, and 64% by the end of November, the median clearly falls during November. Then using proportions (50–47)/(64–47) gives 17.7%, the relative distance into November. Thus the median lies 17.7% into November (month 11), calculated as 11.177 (and rounded to 11.2 for presentation, i.e. a precision of

about three days). The 5th and 95th percentiles were interpolated in a similar fashion. Dates in January were recorded as being in month 1 (not month 0).

Ringing data were collected by ringers in the standard SAFRING (South African Bird Ringing Unit) electronic format. This includes standard ringing information (such as location and date) and data on bird body mass, wing length and primary moult (de Beer *et al.* 2001). Ringing and recapture records submitted to SAFRING from 1998 to 2003 for adults of the three species were extracted from the database.

Primary moult records were extracted from SAFRING's database for all three species in the Western Cape, KwaZulu-Natal and Gauteng Provinces (Figure 1). Data were taken from one-by-one degree grid cells to reduce geographic effects within provinces, except in Gauteng where data from grids 2528 and 2627 were combined. In all cases except one, extraction of data was restricted to the period from September 1998 to September 2004. For Cape Weavers in KwaZulu-Natal, records from 1992 onwards were included so that the number of records would be sufficient for the Underhill and Zucchini (1988) moult model to converge. Timing and duration of moult parameters were compared to breeding seasonality. Results were compared with those published for these three species in the Eastern Cape (Craig *et al.* 2001).

In the three species, moult of the primaries is ascendant, with the feathers renewed from one to nine outwards. The relative masses of each primary (as described in Underhill and Summers 1993) were obtained from published sources: Cape Weaver (Underhill and Joubert 1995), Southern Masked Weaver (Oschadleus *et al.* 2000) and Southern Red Bishop (Craig *et al.* 2001). Underhill and Joubert (1995) showed that small samples are adequate to determine the relative masses of primary feathers because there is little intra-specific variation in this characteristic. The Underhill-Zucchini moult model (Underhill and Zucchini 1988), developed to estimate start and duration of primary moult, was applied to the data sets. The data were considered to be of 'type 2' of the model, because full moult scores were recorded for each bird and all birds were considered available for sampling throughout the moult period. The parameters of primary moult were estimated using the transformations recommended by Summers *et al.* (1980, 1983), designed to reduce the bias introduced by the fact that the individual feathers are of different masses. The moult index used was percentage feather mass grown (PFMG), calculated from the

moult score for the individual feathers according to the method of Underhill and Summers (1993).

Results

The range for egg-laying months (5th and 95th percentiles) is shortest in Southern Red Bishops (1.4–6.5 months, mean 3.3 months), intermediate in Cape Weavers (2.7–5.3 months, mean 3.9 months) and greatest in Southern Masked Weavers (3.9–5.4 months, mean 4.6 months) (Table 1). By region, the range for egg-laying months was most variable across species in the arid regions, i.e. the Karoo (2.7–6.5 months) and Northern Cape (1.4–4.6).

Peak egg-laying (median) occurred first in the Western Cape for all three species; thereafter the median followed different sequences northwards for the different species. Median egg-laying was similar for Cape and Southern Masked Weavers in the Eastern Cape, Karoo, KwaZulu-Natal and former Transvaal, with the maximum difference in medians being eight days in the Karoo. In the Western Cape the Cape Weaver median breeding time was earlier than that for Southern Masked Weavers by 19 days. In the Karoo records were less seasonal due to irregular rainfall. Southern Red Bishop median egg-laying months lagged behind the median for Cape Weavers in all regions by 3.5 days in KwaZulu-Natal to 46 days in the former Transvaal.

The suggestion made in Craig *et al.* (2001) that later breeding by Southern Red Bishops may be related to nesting sites was tested. The seasonality of nesting habitat use by Southern Masked Weavers were checked in different parts of South Africa, and found that both trees and reeds are used early, as well as throughout, the breeding season by this species (Table 2).

Moulting birds were captured throughout the moulting season (Figure 2); this enabled the moult parameters to be estimated reliably (Table 3). The onset of moult began first (11 November – 2 February) and was longest (3.3–4.1 months) for the Cape Weaver, began later (27 December – 22 March) but was shortest (2.2–2.8 months) for the Southern Masked Weaver, and began latest (13 December – 23 March) and was of intermediate length (2.4–3.1 months) for the Southern Red Bishop.

For the Cape Weaver moult started progressively later along the coast from the Western Cape to KwaZulu-Natal, onset of moult varying from 11 November to 2

February (Table 3). The duration of primary moult varied between regions from 3.3 months to 4.1 months (Table 3). Looking at data from all species and all regions, there is a significant negative correlation of moult start date and duration of moult ($F_{1,16}$=264.4, P<0.05).

The interval between peak breeding (median) and the mean start of primary moult was 1.7–2.2 months in Cape Weavers in the different regions, 3–4.7 months in Southern Masked Weavers, and 2.8–4.4 in Southern Red Bishops (Table 3). This interval was greatest in the Eastern Cape for two species (Southern Masked Weavers and Southern Red Bishops).

Discussion

Breeding duration and seasonality

Breeding seasonality in ploceids seems to depend mainly on rainfall, although different aspects of rainfall may be of differing importance, depending on the region. Over the whole range of the Southern Red Bishop in southern Africa clutches are mostly laid in or shortly after the start of wet season, except in the Western Cape where the peak breeding is after the winter rains (Craig 1982). Rainfall also influences the end of breeding of the Southern Red Bishop; the greater the amount of mid-season rainfall, the later the breeding season ended in the Eastern Cape in different years (Friedl 2004).

Elliott (1973 p 50) suggested that the combination of the end of the rains with rising temperatures is the cue for Cape Weavers in the Western Cape to start breeding, but in the former Transvaal the start of breeding probably depends on the start of the rains. He did not suggest factors affecting the end of breeding, but found some variation in the end of breeding: the last eggs were laid between 9 November and 25 November in four successive seasons in the Western Cape (Elliott 1973, Table 4.3).

The most comprehensive single source of quantitative breeding seasonality data in South Africa is the Nest Record Scheme, held at the Avian Demography Unit. It has not been computerised, thus the latest unpublished analysis (RP Prŷs-Jones and I Newton unpublished data) is used in this study. The range of egg-laying months shows that there is wide variability in length of breeding season across regions and species. This is due to sampling effort and, more importantly, variability in annual rainfall patterns. In arid regions breeding will vary in particular years, giving long

breeding seasons overall. There are several records of early or late breeding by ploceids in response to unusual rainfall (see Craig 1982). In urban areas weavers are able to extend their breeding season every year, as is reflected in the high value of 5.4 months for Southern Masked Weavers in the former Transvaal (Harrison *et al.* 1997).

Cape and Southern Masked Weavers both breed in trees or reeds, while Southern Red Bishops breed chiefly in reeds (Fry and Keith 2004). Craig *et al.* (2001) suggested later breeding by Southern Red Bishops may be related to nesting sites, i.e. reeds may not be available as early as trees are. Southern Masked Weavers, however, breed in reeds as early as they do in trees. Thus reeds should be available to Southern Red Bishops at the same time, yet breeding is delayed. A possible explanation is that reeds used early in the season by Southern Masked Weavers may be dry reeds from the previous season (Brooke 1959), while Southern Red Bishops wait for fresh reeds. The later start of breeding in the Southern Red Bishop compared to the two *Ploceus* species may be due to different cues (aspects of rainfall), e.g. possibly waiting for more cumulative rainfall to fall (Friedl 2002).

Oschadleus *et al.* (2000) found that Southern Masked Weavers in North-west Province started moult on 15 February and moult lasted 80 days. This is similar to the result found here for Gauteng, where moult began on the 11 February and lasted 76 days.

Primary moult and annual cycle

Moult was earliest in the Western Cape winter-rainfall region for all three species, as found by Bonnevie *et al.* (2004) for Southern Red Bishops. In the summer-rainfall region (KwaZulu-Natal and Gauteng), moult started in late January to mid February for the *Ploceus* weavers and in late March for the bishop. Start of moult was most divergent between the three species in the Eastern Cape, varying by nearly four months (Table 3).

For the three ploceids, in all regions studied, primary moult started on average in the same month that the last eggs were laid (Figure 2). Because the breeding cycle takes about a month to complete (incubation plus nestling periods), breeding and moult may overlap in the population, but this is unlikely to apply to individuals. These ploceids follow the normal pattern of a complete moult soon after breeding (Payne 1972). In the Eastern Cape, however, there seems to be a delay between the end of breeding and the start of primary moult for Southern Masked Weavers and Southern

Red Bishops as shown by the relatively large interval between peak breeding and start of moult of over four months (Table 3). Moult parameters are usually considered more fixed than timing of breeding in a passerine's annual life-cycle (King 1973, Snow 1976). Further research is needed to investigate the reasons for the delay between breeding and moult in these two species in the Eastern Cape.

The Cape and Southern Masked Weavers have the same peak breeding seasons in all regions except the Western Cape, but primary moult in Southern Masked Weavers consistently starts later (greater interval between peak breeding and start of moult). The Cape Weaver has a shorter breeding season (shorter range of egg-laying months) than the other two species, suggesting a more synchronised breeding season and thus ability to time moult sooner after breeding. Larger colonies in Cape Weavers than in Southern Masked Weavers may be a mechanism to synchronise breeding: Cape Weavers breed in single-male colonies or in colonies of 2–20 males, while Southern Masked Weavers usually breed in single-male colonies and rarely in colonies with 2–9 males (Tarboton 2001).

Termination of primary moult varied widely in the different regions for each species. This is in sharp contrast to the pattern in Red-billed Quelea *Quelea quelea* which show a high degree of synchronisation in end of moult (Chapter 4). The Red-billed Quelea may need to complete moult before starting the return migration (see Chapter 4) whereas the weavers covered in this chapter are resident and can schedule moult onset and termination according to local environmental conditions. There is, however, a significant negative correlation of moult start date and duration of moult, i.e. the later moult starts the shorter is the duration of moult. This indicates that the weavers covered in this chapter do try to complete moult sooner if they started moult later. In Cape White-eyes *Zosterops pallidus* duration of moult is fixed in different regions of South Africa, and may be a species-specific trait in this species. Onset of moult follows breeding and is one month earlier in the Western Cape than in the Free State and Eastern Cape (Hulley *et al.* 2004). The weavers studied here show variation in timing and duration of both breeding and moult parameters, suggesting adaptability to local environmental conditions, irrespective of day-length.

Range expansion and moult

The median date of egg-laying in Cape and Southern Masked Weavers was similar throughout South Africa (Table 1), but Southern Masked Weavers breed 0.6 months

later than Cape Weavers in the Western Cape. In recent decades, the Southern Masked Weaver expanded its range into the south-western part of the Western Cape. Oschadleus *et al.* (2000) found that Southern Masked Weavers in the Western Cape started moult 9 January and lasted 74 days, while in this study moult started 27 December and lasted 84 days. The data set used by Oschadleus *et al.* (2000) was from 1988 to 1995, while in this study the data was from 1998 to 2004. Southern Masked Weavers in the Western Cape appear to have advanced the start of primary moult by about two weeks. Monitoring, e.g. the nest Record Scheme, in future decades will show if the Southern Masked Weaver continues to advance its peak breeding season in the Western Cape to match that of the Cape Weaver. The duration of primary moult differed widely (74 and 84 days) but the 74 days recorded by Oschadleus *et al.* (2000) had a large standard error of 13 days associated with that duration.

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Table 1: Months of egg-laying (percentages) for Cape Weaver, Southern Masked Weaver and Southern Red Bishop in South Africa (from Prŷs-Jones and Newton unpublished data). For Southern Masked Weavers additional breeding records from northern KwaZulu-Natal are included. The percentages are summarized as 5th percentile (represents start of moult), 95th percentiles (end of moult), range (90% range of months of egg-laying) and median egg-laying month; numbers represent parts of months, e.g. 12.5 = mid December, 12.4 = 40% through December WC=Western Cape, EC=Eastern Cape, KZN=KwaZulu-Natal, Tvl= former Transvaal (this region incorporates the current Gauteng Province), NC=Northern Cape

Species	Area	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	n	5th	95th	Range	Median
Cape Weaver																		
	EC	2	5	4	13	21	35	15	2		1	1		97	7.6	12.9	5.3	11.1
	Karoo				38	35	27							48	9.1	11.8	2.7	10.4
	KZN			1	1	5	22	58	13					148	10.7	1.6	2.9	12.4
	Tvl			8	14	22	23	25	9					65	8.6	1.4	4.8	11.3
	WC	3	12	30	25	28	3							1225	7.2	10.9	3.7	9.2
Southern Masked Weaver																		
	EC			2	23	23	32	16	5					44	9.1	1.0	3.9	11.1
	FS				9	29	34	12	15	1				82	9.6	1.7	4.2	11.4
	Karoo		1	9	14	42	16	11	2			1	2	85	8.4	1.5	5.1	10.6
	KZN				15	2	3	55	25					89	9.3	1.8	4.5	12.5
	NC						34	31	13		22			32	11.1	3.8	4.6	12.5
	Tvl		<1	6	14	20	27	18	10	5	<1		<1	512	8.8	2.2	5.4	11.4
	WC		1	15	40	14	20	9	1					205	8.3	12.6	4.3	9.8
Southern Red Bishop																		
	EC				1	3	15	58	14	8	2			160	11.1	2.6	3.5	12.6
	FS						3	36	56	4	<1	<1		240	12.1	2.0	1.9	1.2
	Karoo			2	6	34	4		1	6	43	3		96	9.5	4.0	6.5	2.3
	KZN					6	12	67	13	1	1			1276	10.8	1.8	2.9	12.5
	NC					5	86	9						22	11.0	12.4	1.4	11.5
	Tvl					2	20	34	30	10	4			1043	11.2	2.9	3.7	12.8
	WC		<1	18	47	25	10	<1						1109	8.3	11.5	3.2	9.7

Table 2: Breeding habitat (percentages) for Southern Masked Weavers in South Africa (from the Nest Record Cards) SWC=south-western Cape, WC=Western Cape (excluding SWC), EC=Eastern Cape, KZN=KwaZulu-Natal, FS=Free State, Tvl=former Transvaal

Area	Species	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Totals
SWC	reeds		<1	12	36	9	27	14	1					222
	trees		2	11	43	38	4	2						47
WC	reeds			4	46	18	14	14			4			28
	trees			5	25	25	18	13	2		7	2	4	56
EC	reeds			10	30	30	30							10
	trees				15	48	17	15	4					52
KZN	reeds													0
	trees					50	25	13	13					8
FS	reeds				50	10	10		30					10
	trees					15	41	11	30	4				27
Tvl	reeds				14	40	23	3	17	3				70
	trees			6	9	21	24	19	13	6		2		224

Table 3: Estimates of the primary moult parameters of adult Cape Weavers, Southern Red Bishops and Southern Masked Weavers in South Africa, 1998–2003. The final column gives the estimated difference between the median egg-laying date and the mean date of start of moult

EC data are from Craig *et al.* (2001); * data from Oschadleus *et al.* (2000)

Localities are abbreviations for South African provinces: WC=Western Cape, EC=Eastern Cape, KZN=KwaZulu-Natal, GP=Gauteng, MP=Mpumulanga, FS=Free State, NW=North-west Province; and one degree grid cell in which the data were collected

Locality	Mean starting date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Standard error (days)	Mean completion date	Standard error (days)	n	Mean moult — peak breed (months)
Cape Weaver										
WC, 3318	11 Nov	1.4	24.2	0.6	98.1	2.0	17 Feb	1.3	3226	2.1
EC	9 Jan	4	25.2	2.1	106	7	25 Apr	4.7	316	2.2
KZN, 2930	2 Feb	4.1	31.5	2.7	124.2	9.5	6 Jun	7.4	238	1.7
Southern Masked Weaver										
WC, 3318	27 Dec	2.4	33.2	1.2	84.4	3.3	22 Mar	2.2	1411	3.1
EC	22 Mar	3	24.8	1.9	67	5	28 May	3.6	391	4.7
GP	11 Feb	0.9	18.8	0.6	75.9	1.7	28 Apr	1.3	2556	3.0
WC *	9 Jan	7.5	24.0	2.1	73.8	13.2	24 Mar	6.5	2318	
NW *	15 Feb	2.7	22.7	1.6	80.4	3.9	7 May	2.5	1547	
Southern Red Bishop										
WC, 3318	13 Dec	1.1	25.3	0.6	88.6	1.7	12 Mar	1.2	3154	2.8
EC	28 Apr	4	47.3	2.9	89	7	26 Jul	6.1	622	4.4
GP	23 Mar	1.5	35.1	1.1	71.9	2.5	3 Jun	2.3	4808	2.9

Figure 1: Capture sites of adult Cape Weavers, Southern Masked Weavers and Southern Red Bishops in selected areas in South Africa, 1998–2003. Dots show sites from which primary moult data were obtained; the data from Craig *et al.* (2001) for the Eastern Cape was centred on Grahamstown. All the quarter-degree grid cells in South Africa in which Cape Weavers were recorded during the Southern African Bird Atlas Project are shaded (Mundy and Herremans 1997); Southern Masked Weavers and Southern Red Bishops are found nearly throughout the region.

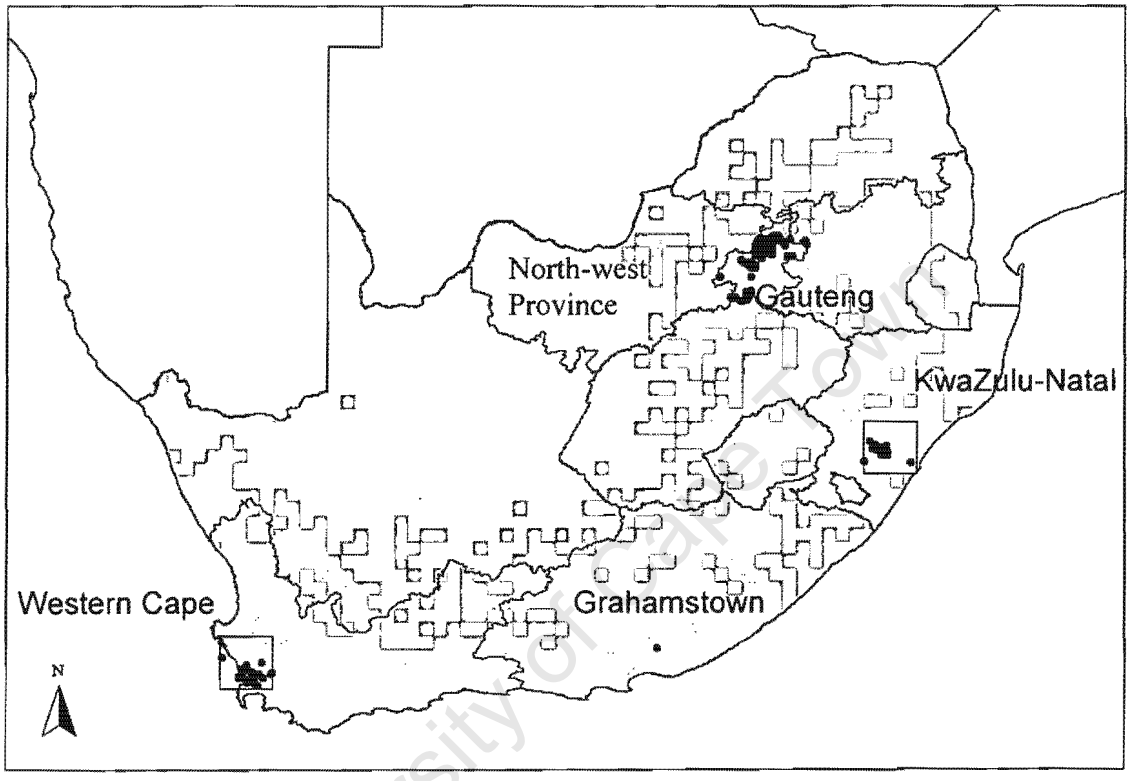
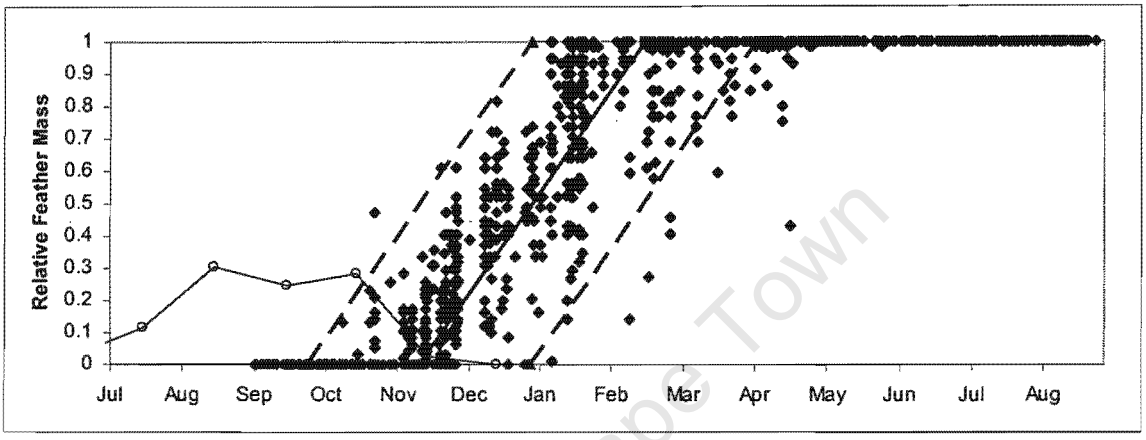
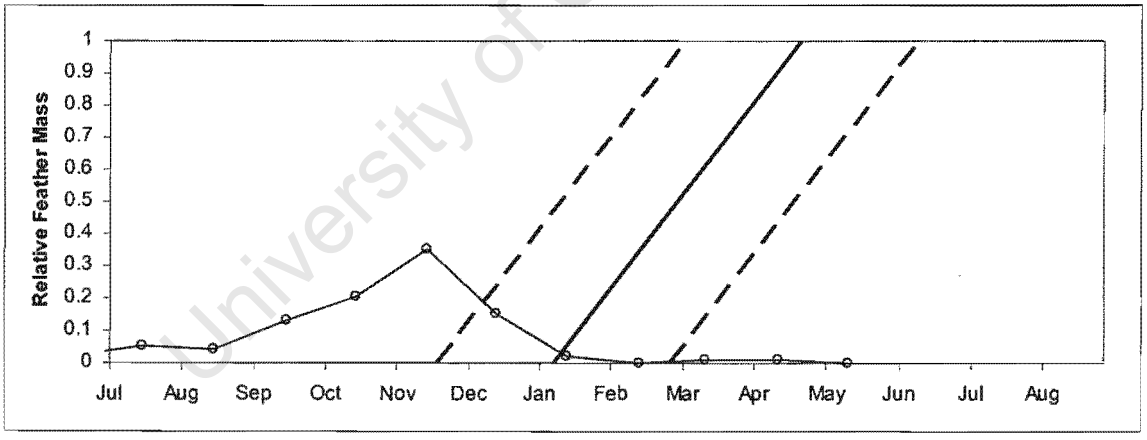


Figure 2: Timing of egg-laying and primary moult for adult weavers in different parts of South Africa; the open circles with thin solid line shows the proportion of eggs laid per month (from the Nest Record Cards summary by Prŷs-Jones and Newton unpublished data); the solid diamonds represent relative feather mass values by date; the solid diagonal line joins the estimated mean start and end dates of moult, while the diagonal dotted lines show the approximate 95% confidence intervals of moult scores on any given date. Original moult data for the Eastern Cape are not available, hence only mean and confidence lines are shown

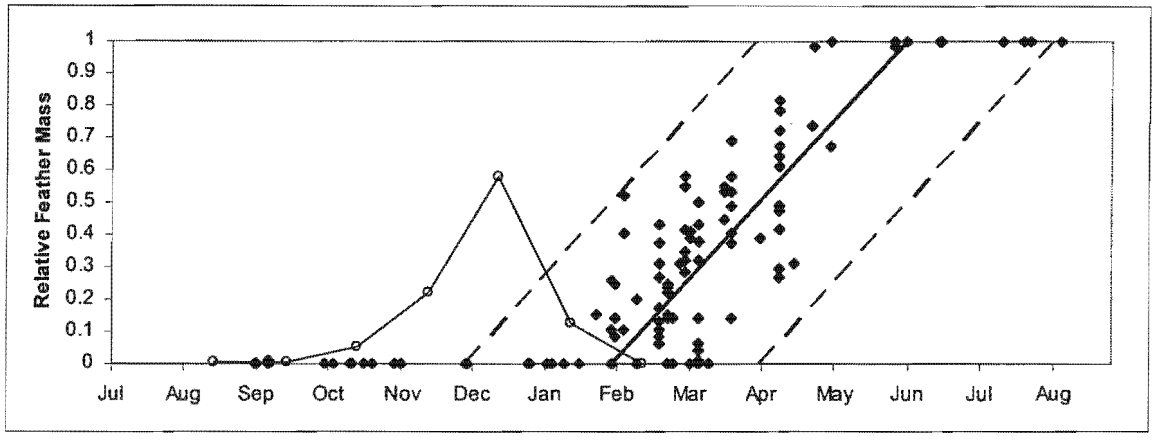
(a) Cape Weaver, breeding and moult records in the Western Cape



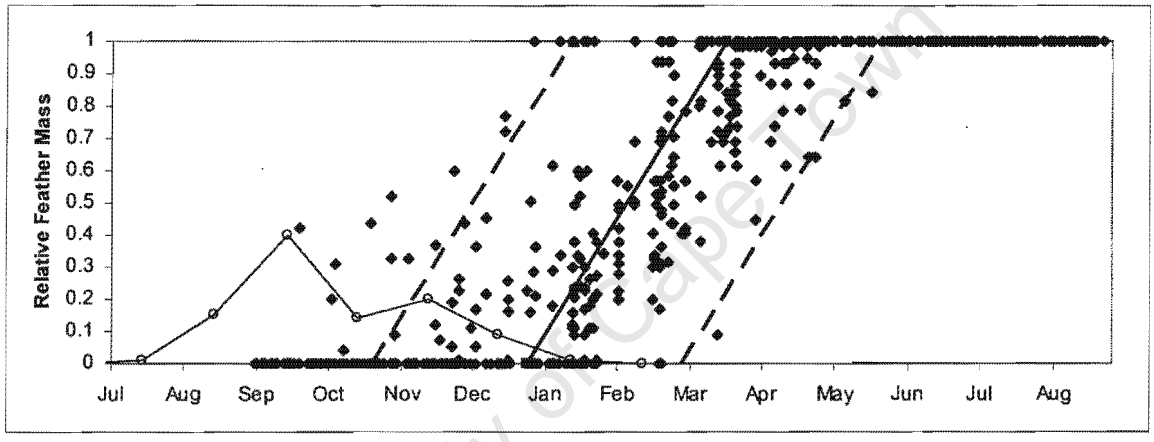
(b) Cape Weaver, breeding records and moult parameters in the Eastern Cape



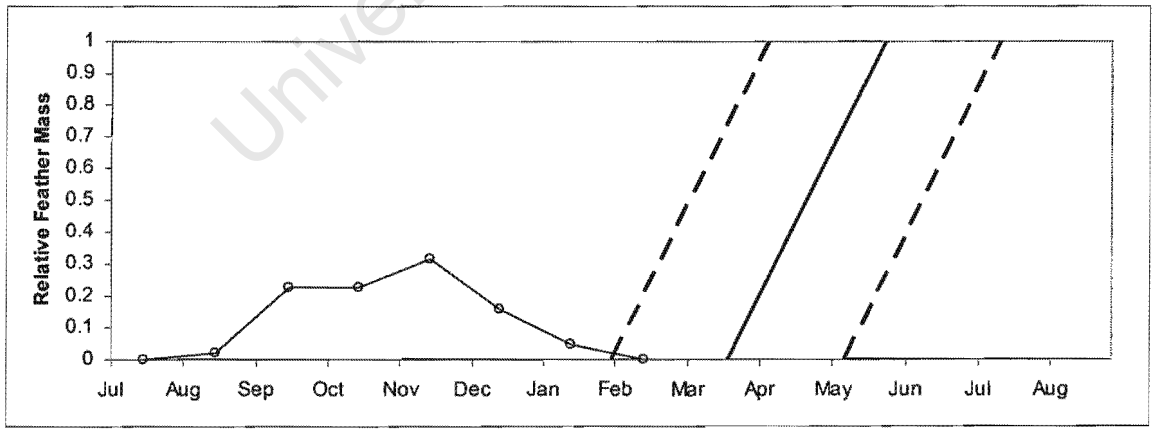
(c) Cape Weaver, breeding and moult records in KwaZulu-Natal



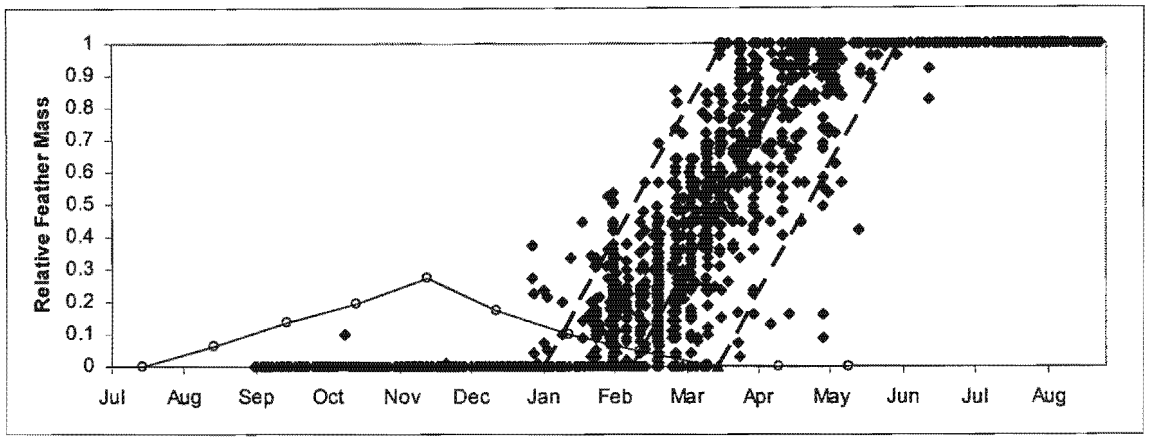
(d) Southern Masked Weaver, breeding and moult records in the Western Cape



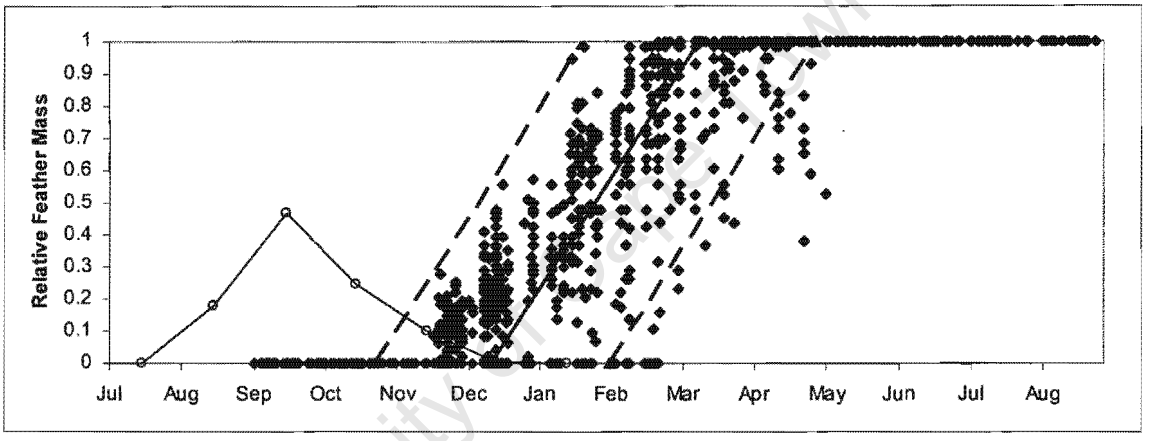
(e) Southern Masked Weaver, breeding records and moult parameters in the Eastern Cape



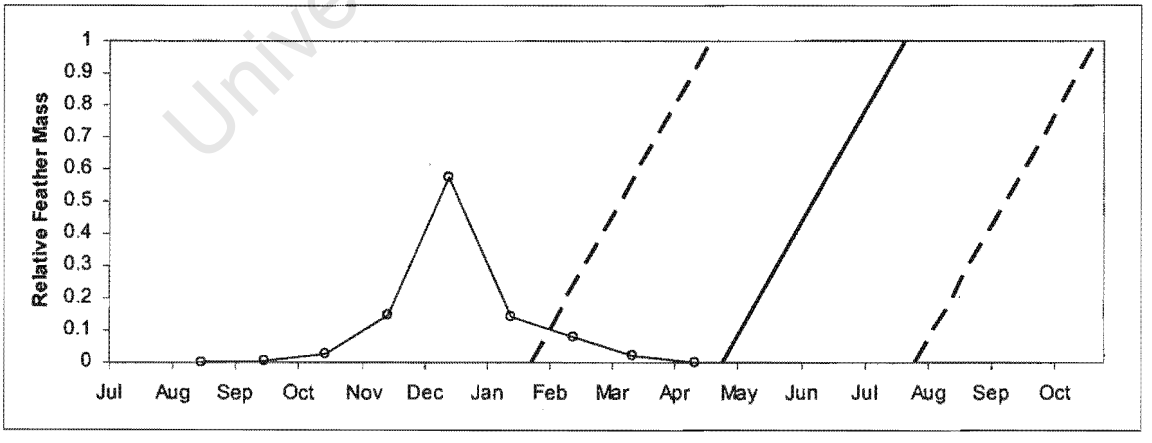
(f) Southern Masked Weaver, breeding records in former Transvaal and moult records in Gauteng



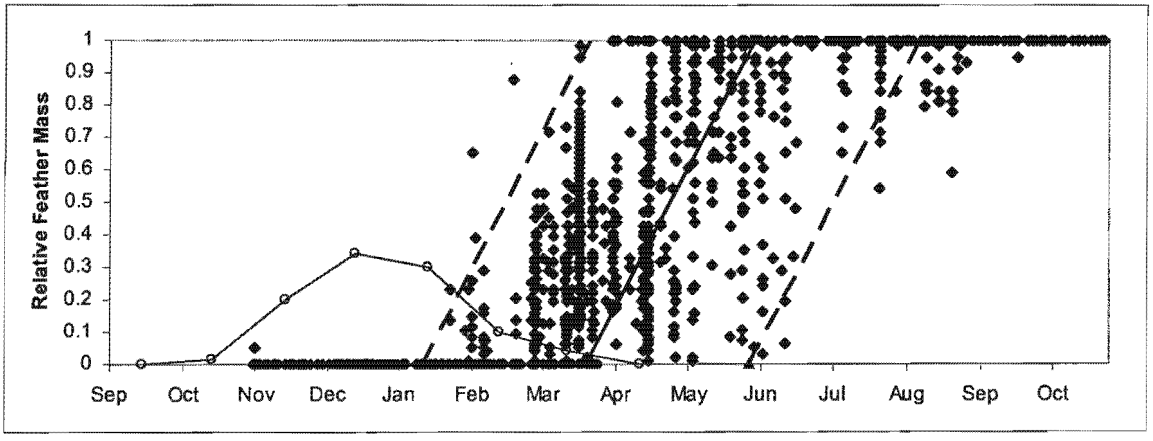
(g) Southern Red Bishop, breeding and moult records in the Western Cape



(h) Southern Red Bishop, breeding records and moult parameters in the Eastern Cape



(i) Southern Red Bishop, breeding records in former Transvaal and moult records in Gauteng



Chapter 6

Breeding seasonality and primary moult parameters in *Euplectes* species in South Africa

Breeding seasonality and primary moult parameters in *Euplectes* species in South Africa

Abstract

Bishops and widows are fairly uniform in their ecology, but breed in different micro-habitats. The grassland biome in South Africa has a summer rainfall and Long-tailed *Euplectes progne*, White-winged *E. albonotatus*, Red-collared *E. ardens*, and Fan-tailed Widows *E. axillaris* bred from October or November to March. Primary moult started in late March or early April. The widows with long tails (Long-tailed and Red-collared Widows) had moult durations of two months, while the widows with shorter tails (White-winged and Fan-tailed Widows) had moult durations of 1.5–1.7 months. Moult ended in late May or early June. Long-tailed Widows have rounder wings than other weaver species, possibly because their larger size affects flight aerodynamics. Southern Red Bishops *E. orix* and Yellow Bishops *E. capensis* in the Western Cape experience winter rainfall and breed after the rains. In these two species breeding was mainly from August to November and moult started in December. Primary moult duration in the Yellow Bishop was relatively long at 3.4 months. Yellow Bishops grew individual primary feathers at an average rate of 21.3 days per feather, while the other species moulted primaries more quickly: White-winged Widow 8.1 days, Fan-tailed Widow 11.3 days and Red-collared Widow 14.4 days. The number of primaries growing simultaneously was similar in the different species.

Introduction

There are seven breeding species of *Euplectes* bishops and widows in South Africa (Tarboton 2001). The bishops have short tails that are not replaced during the pre-nuptial moult, and the widows grow long black tails in the pre-nuptial moult (Craig 1993). Species in this genus in South Africa have their distributions centred on the grassland and savanna biomes in eastern part of the country; Southern Red Bishop *Euplectes orix* and Yellow Bishop *E. capensis* extend into the fynbos region of the Western Cape (Harrison *et al.* 1997, Figure 1). All seven South African species occur in the two easternmost provinces, KwaZulu-Natal and Mpumulanga; six species occur

in Limpopo Province, Gauteng and the Eastern Cape; five species in North-west and Free State; three in the Western Cape; and one, the Southern Red Bishop, in the Northern Cape.

The species are fairly uniform in their ecology and maintain mutually exclusive territories where they occur in the same area (Emlen 1957, Craig 1980). They are common birds of grassland or marshes, feeding mainly on seeds. They are sexually and seasonally dimorphic; breeding males have black plumage with either red or yellow agonistic signals. The females are dull-coloured through the year. Male widows have elongated black tail feathers which are used in mate selection. Tail length in male widows in breeding plumage varies greatly between species from 65 mm in Fan-tailed Widows *E. axillaris* to 500 mm in Long-tailed Widows *E. progne* (Andersson and Andersson 1994, Pryke 2003). All species feed and roost in large flocks in the non-breeding season, often in mixed-species flocks (Craig 1980).

The Southern Red Bishop and Yellow Bishop breed from September to November in the Western Cape, about three months earlier than the peak from December to March in the summer rainfall region. The other *Euplectes* species breed mainly from October to March (Harrison *et al.* 1997). All *Euplectes* species are polygynous, build a dome-shaped nest with a side entrance, and the female alone incubates eggs and feeds young (Fry and Keith 2004).

Little is known about the moult of bishops and widows. Craig and Manson (1979) found that three *Euplectes* species in KwaZulu-Natal and Zimbabwe moulted soon after breeding; the authors estimated duration of primary moult based on recaptures. Bonnevie *et al.* (2004) found that Southern Red Bishops moulted three months earlier in the Western Cape than in the predominantly summer rainfall regions. Savalli (1993) described the prenuptial moult in Yellow-mantled Widowbird *E. macrourus* in western Kenya.

In this paper, primary moult parameters were estimated for five additional species: Long-tailed Widow, White-winged Widow *E. albonotatus*, Red-collared Widow *E. ardens*, Fan-tailed Widow, and Yellow Bishop. Southern Red Bishop data was analysed in Chapter 5 but is compared to the other *Euplectes* species in this chapter. There was insufficient moult data for Yellow-crowned Bishop *E. afer*. Moult parameters are usually considered to be more fixed than the timing of breeding in a passerine's annual life-cycle (Snow 1976). This paper examines the relationship

between the timing of primary moult and the timing of breeding in the annual cycles of the widows of South Africa.

Methods

Breeding seasonality data were obtained from the BirdLife South Africa Nest Record Card Scheme (NRC) (RP Prŷs-Jones and I Newton unpublished data; Underhill *et al.* 1991). Prŷs-Jones and Newton (unpublished data) estimated the month of laying of the first egg for each record. They then summarised breeding seasonality for all birds in South Africa by presenting monthly totals of clutches laid per species per region. One of the regions they used was the former Transvaal province: this region incorporates the current Gauteng Province, from where most of the records originate anyway. To compare breeding seasonality of weavers, the tabulated data of Prŷs-Jones and Newton were used to estimate the median and the 5th and 95th percentiles for each species and region. The median was calculated by finding the cumulative monthly sums of the percentage of nest records. The median month was the month in which the cumulative sum first exceeded 50%. The values of the sums of the previous and successive months were used to assign a relative distance into the month. For example, if there were 47% of cumulative records by the end of October, and 64% by the end of November, the median clearly is during November. Then using proportions (50–47)/(64–47) gives 17.7%, the relative distance into November. Thus the median lies 17.7% into November (month 11), calculated as 11.177 (and rounded to 11.2 for presentation, i.e. a precision of about three days). The 5th and 95th percentiles were interpolated in a similar fashion. Dates in January were recorded as being in month 1 (not month 0).

Ringing data were collected by ringers in the standard SAFRING (South African Bird Ringing Unit) electronic format. This includes standard ringing information (such as location and date) and data on bird body mass, wing length and primary moult (de Beer *et al.* 2001). Primary moult records were extracted from SAFRING's database until mid-January 2005 for adult *Euplectes* species. Moult in Southern Red Bishops was analysed in Chapter 5. For each species, a geographic area was chosen so that sufficient records could be obtained for the analysis of moult: generally 200 records spread over a year allow the Underhill-Zucchini model to

converge. In all species moult of the primaries is ascendant, with the feathers renewed from one to nine outwards.

To determine the relative mass of each primary, as described in Underhill and Summers (1993), the primaries of one White-winged Widow and two Long-tailed Widow specimens were used. The White-winged Widow male was a road-kill I found at Skeerpoort, North-west Province. One Long-tailed Widow (non-breeding male) was a road-kill found in Wakkerstroom, Mpumulanga, by Kevin McKann. The other (breeding male) was a road-kill I found in Leandra, Mpumulanga. The primaries were dried in an oven at 60°C for 24 hours to eliminate moisture and weighed (Ohaus GA200D balance, precision 0.0001g). These values were averaged and used for to calculate the relative mass of each primary. Underhill and Joubert (1995) showed that small samples are adequate to determine the relative masses of primary feathers because there is little intra-specific variation in this characteristic; they also showed that within the Charadriiformes, the relative masses of the primary feathers were so similar that the average value for the species for which data were available could safely be used for species for which data were unavailable. The Underhill-Zucchini moult model (Underhill and Zucchini 1988), developed to estimate start and duration of primary moult, was applied to the data sets. The data were considered to be of 'type 2' of Underhill and Zucchini (1988), because full moult scores were recorded for each bird and all birds were considered available for sampling throughout the moult period. The use of type 2 data assumes that the sample of birds handled on each day is representative of the stages of primary moult in the population on that day. The parameters of primary moult were estimated using the transformations recommended by Summers *et al.* (1980, 1983), designed to reduce the bias introduced by the fact that the individual feathers are of different masses. The moult index used was percentage feather mass grown (PFMG), calculated from the moult score for the individual feathers according to the method of Underhill and Summers (1993). This analysis was then repeated to provide estimates of the parameters of moult of each individual primary (Underhill 2003, Underhill *et al.* in press). The PMFG for White-winged Widows were used for Red-collared Widow, Fan-tailed Widow and Yellow Bishop because wings of these species were unavailable.

For Long-tailed Widows all moult records were pooled (166 records from Mpumulanga, 55 from Free State, 53 from Gauteng, and five records from other provinces). For White-winged Widows, 686 records from Gauteng were used. For

Red-collared Widows, 667 records from Gauteng were used. For Fan-tailed Widows, 1002 records from a one-by-one degree block in KwaZulu-Natal were used. For Yellow Bishops, 777 records from two adjacent one-by-one degree blocks in the Western Cape were used (Figure 2).

Results

Breeding by *Euplectes* species begins earliest in the Western Cape, the median date of egg-laying in this province being September (Table 2). In the grassland biome breeding is in summer: in KwaZulu-Natal median date of egg-laying is in December for all species, and in the former Transvaal it is December or January (Table 2). Median date for onset of egg-laying is variable in the other regions.

Relative feather masses are similar for most Ploceidae weavers (unpublished data; see Chapter 9), as exemplified by Southern Red Bishop and White-winged Widow (Figure 3). The wing shape (by primary feather mass) is different, however, in Long-tailed Widows and in Thick-billed Weavers *Amblyospiza albifrons* which have a more rounded wing with the outer primaries decreasing in size. For the Red-collared Widow, Fan-tailed Widow and Yellow Bishop, wings were not available, so two models were tested using the relative masses of both types of widow wing shapes, i.e. using that of the White-winged Widows and of the Long-tailed Widows. Using the White-winged Widow relative masses gave acceptable results for all three species tested. Using the Long-tailed Widow PFMG did not always give acceptable results, and thus this model was excluded.

Primary moult follows soon after breeding in all species (Tables 2 and 3). Moulting birds were captured throughout the moulting season (Figure 4), sometimes in large numbers; this enabled moult parameters to be estimated reliably. *Euplectes* species breeding in summer rainfall areas (Long-tailed Widow, White-winged Widow, Red-collared Widow and Fan-tailed Widow) had primary moult durations of about two months, starting in late March or early April and ending in late May or early June. The Southern Red Bishop had a moult duration of 2.4 -3.0 months. The Yellow Bishop showed longer duration of 3.4 months, with moult starting in early December (Table 3).

The estimated time for individual feathers to grow varied as follows (Table 4): White-winged Widow, 5–13 days; Red-collared Widow, 9–18 days; Fan-tailed

Widow, 6–18 days; and Yellow Bishop, 14–29 days (Table 3). For Long-tailed Widow, the sample sizes were too small to allow individual feather durations to be estimated. Numbers of primaries growing simultaneously were similar in the five species: Long-tailed Widow 2.2, White-winged Widow 1.9, Red-collared Widow 2.3, Fan-tailed Widow 2.2, and Yellow Bishop 2.0. The start and end dates for individual primaries (Table 4) with that for the whole wing (Table 3) match best for Red-collared Widow (6 April for start of primary 1 versus 5 April for whole wing), and worst for Fan-tailed Widow and Yellow Bishop (7 days difference).

Discussion

The different wing shapes of the Long-tailed Widow compared to Southern Red Bishop and White-winged Widow are probably due to adaptation rather than phylogeny (Dawson 2005). For a range of European passerines, Dawson (2005) found that the greater relative mass of the outer primaries in some species may reflect a protective function against physical abrasion, or an aerodynamic function in that each of these feathers provides a leading edge to the wing. Scaling relationships (log mass/log length) were related to flight characteristics and habitat, rather than to phylogeny (Dawson 2005). European Starlings *Sturnus vulgaris,* with more rounded wingtips, tended to take off from the ground at a steeper angle of ascent than those with relatively more pointed wingtips (Swaddle and Lockwood 2003). The widows all have a similar ecology but the Long-tailed Widow is considerably larger than other *Euplectes* species, and this may impact on the aerodynamics of its flight, and thus wing-shape. Long-tailed Widow males have tails that are much larger than those of the females and there may be a sexual difference in the relative feather masses – more specimens are needed to determine this.

Breeding seasonality in widows and bishops in summer rainfall areas is well-defined. Start of moult is 2.5–3.5 months after peak egg-laying, and 0.9–1.7 months after 95th percentile of breeding (Table 5). One breeding cycle consisting of the incubation and nestling periods is three to four weeks in all the *Euplectes* species (Table 5); the number of broods per season is less well known.

Euplectes bishops and widows are largely grassland birds, although Yellow Bishop is found more in fynbos and montane habitats, and thus have fairly similar distributions; the core of their ranges, as indicated by the areas of high reporting rates,

are concentrated in the areas where grassland occurs (Figure 1). Duration of primary moult is similar in the grassland species (two months or less), but Yellow Bishops take nearly three and a half months to complete moult. Onset of moult is similar in the summer rainfall species (late March or April). Yellow Bishops start moult earlier in the winter rainfall region, as do Southern Red Bishops, Cape and Southern Masked Weavers (Oschadleus *et al.* 2000, Chapter 5). The Southern Red Bishop has a wider distribution than other *Euplectes* species and has a moult duration of 72 to 89 days (Craig *et al.* 2001, Bonnevie 2004, Chapter 5). In the winter rainfall region of the Western Cape, the primary moult of the Southern Red Bishop started about three months earlier than in the summer rainfall regions, but in all regions the onset of moult commenced at the end of the breeding season (Bonnevie 2004, Chapter 5).

Nuttall (1993) studied the breeding seasonality of four co-occurring species of widow in grassland habitat near Pietermaritzburg, KwaZulu-Natal. Long-tailed Widows developed breeding plumage earliest, and retained it for the longest period of time, followed by Fan-tailed Widow. White-winged and Red-collared Widows exhibited breeding plumage for the shortest periods (Nuttall 1993). Nuttall's (1993) study related to body moult but there is a similarity with wing-moult: in this study Long-tailed and Red-collared Widows had moult durations of two months, while that of White-winged Widows was 1.5 months.

Craig and Manson (1979) made preliminary estimates of the parameters of primary moult from a small sample of recaptures and from the numbers of simultaneously growing primaries in KwaZulu-Natal and Zimbabwe. They estimated duration of moult to be 110 days in Southern Red Bishops, 100 days in male Fan-tailed Widows, and 80 days for Red-collared Widows and female Fan-tailed Widows. These durations are longer than the 47–61 days estimated in the present study for widows in the summer rainfall region.

Adult Yellow Bishops needed 2–4 weeks to grow individual primaries, while the other species moulted individual primaries more quickly. The estimated durations of moult of the individual primaries showed considerable variation; this variation is more likely to be attributable to sampling variation than to biological processes. The number of birds in moult for each primary feather were mostly small. The average of the individual primary durations for a species is however likely to provide a useful characteristic of the species.

The estimated overall duration of primary moult (Table 4) was closely correlation with the interval between the estimated starting date of moult of the first primary to the estimated completion date of moult of the ninth (outermost) primary (Table 3). The estimated starting date of primary moult of Red-collared Widows, for instance, in the overall analysis was 5 April (Table 3) and the estimate starting date for the first primary was 6 April (Table 4b); the overall moult ended on 3 June and the moult of the ninth primary was completed on 4 June. Also the number of primaries growing simultaneously was similar in the different species, indicating relatively uniform growth rates in the different species. Yellow Bishops achieve a long moult duration by growing individual primaries at a slower rate than do other *Euplectes* species, and not by growing fewer primaries simultaneously, as do Sociable Weavers (Chapter 2).

It would be useful to have the relative primary masses of all *Euplectes* species to confirm the results in this study. The South African *Euplectes* species for which primary moult parameters remains unknown is Yellow-crowned Bishop *E. afer*.

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Table 1: Individual primary feather masses (g) of two Long-tailed Widow specimens from Mpumulanga and one White-winged Widow specimen from North-west Province, and the mean relative mass of each primary, used in the calculation of Percentage Feather Mass Grown

Primary	Feather mass (g)			Mean relative feather masses	
	Long-tailed Widow male, left wing	Long-tailed Widow male, right wing	White-winged Widow male, left wing	Long-tailed Widow	White-winged Widow
1	0.0235	0.0356	0.0108	9.4	9.3
2	0.0234	0.0372	0.0112	9.5	9.6
3	0.0250	0.0400	0.0114	10.2	9.8
4	0.0275	0.0440	0.0121	11.3	10.4
5	0.0289	0.0466	0.0135	11.9	11.6
6	0.0305	0.0484	0.0138	12.4	11.8
7	0.0314	0.0468	0.0140	12.4	12.0
8	0.0304	0.0433	0.0146	11.7	12.5
9	0.0295	0.0378	0.0152	10.8	13.0
10	0.0009	0.0014	<0.0001	0.4	0.0
Total	0.2510	0.3811	0.1166	100.0	100.0

Table 2: Months of egg-laying (percentages) for *Euplectes* species in South Africa (from Prŷs-Jones and Newton unpublished data). The percentages are summarized as 5th percentile (represents start of moult), 95th percentiles (end of moult), range (90% range of egg-laying) and median egg-laying month; numbers represent parts of months, e.g. 12.4 = 40% through December (see text)
WC=Western Cape, EC=Eastern Cape, NC=Northern Cape, KZN=KwaZulu-Natal, FS=Free State, Tvl=former Transvaal (includes Gauteng)

Species	Locality	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	n	5th	95th	Range	Median
Southern Red Bishop																		
	EC			1	3	15	58	14	8	2				160	11.1	2.6	3.5	12.6
	FS					3	36	56	4	<1	<1			240	12.1	2.0	1.9	1.2
	Karoo		2	6	34	4		1	6	43	3			96	9.5	4.0	6.5	2.3
	KZN				6	12	67	13	1	1				1276	10.8	1.8	2.9	12.5
	NC				5	86	9							22	11.0	12.5	1.4	11.5
	Tvl				2	20	34	30	10	4				1043	11.2	2.9	3.8	12.8
	WC	<1	18	47	25	10	<1							1109	8.3	11.5	3.3	9.7
Yellow-crowned Bishop																		
	EC						13	27	7	47	7			15	12.4	4.3	3.9	3.1
	FS					6	53	12	24	6				17	11.9	3.2	3.3	12.8
	Tvl					1	19	54	13	11	2			104	12.2	3.7	3.5	1.6
Yellow Bishop																		
	EC			9	18		45	18	9					11	9.6	2.5	4.9	12.5
	KZN					10	80	10						10	11.5	1.5	2.0	12.5
	WC	<1	23	44	26	5	1							239	8.2	11.2	3.0	9.6
Fan-tailed Widow																		
	EC					25	50		25					16	11.2	2.8	3.6	12.5
	KZN			4	5	24	40	18	7	1				148	10.2	2.5	4.3	12.4
White-winged Widow																		
	KZN					13	41	38	6		3			32	11.4	2.7	3.3	12.9
	Tvl				1	4	37	26	29	3				70	11.8	2.9	3.1	1.3
Red-collared Widow																		
	EC			14	25	32	7	4	18					28	9.4	2.7	5.4	11.3
	KZN				17	31	36	13	2	2				64	10.3	1.9	3.6	12.0
	Tvl				4	18	46	25	4	4				28	11.1	2.6	3.5	12.6
Long-tailed Widow																		
	EC			20	45	25		10						20	9.3	1.5	4.3	10.7
	FS				9	45	26	6	13	1				152	10.5	2.7	4.2	11.9
	KZN			3		38	25	22	13					32	11.1	2.6	3.6	12.4
	Tvl				7	17	30	31	13	2				87	10.7	2.8	4.1	12.9

Table 3: Estimates of the primary moult parameters of adults of five species of widowbirds (Long-tailed Widow, White-winged Widow, Red-collared Widow, Fan-tailed Widow, and Yellow Bishop) in South Africa; Southern Red Bishop data is from Chapter 5
Localities are abbreviations for South African provinces: WC=Western Cape, EC=Eastern Cape, GP=Gauteng, KZN=KwaZulu-Natal; and area in which the data were collected; Gauteng is included in the Transvaal region of Table 2
PFMG model = * indicates that the PFMG data of White-winged Widows was used as wings of the species concerned were not available; Model = blank means that wings of the species concerned were used

Area	PFMG model	Mean starting date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Duration (months)	Standard error (days)	Mean completion date	Standard error (days)	n
Long-tailed Widow											
all		26 Mar	4.8	20.6	2.9	60.7	2.0	8.7	25 May	7.1	279
White-winged Widow											
GP		18 Apr	2.5	26.3	1.6	46.5	1.5	3.3	3 Jun	2.6	685
Red-collared Widow											
GP	*	5 Apr	2.5	30.8	1.6	59.9	2.0	3.5	3 Jun	2.6	667
Fan-tailed Widow											
KZN grid 2930	*	2 Apr	1.9	18.1	0.9	50.5	1.7	2.8	23 May	2.0	1002
Southern Red Bishop											
WC grids 3318 &3418		13 Dec	1.1	25.3	0.6	88.6	3.0	1.7	12 Mar	1.2	3154
GP, 1998-2003		23 Mar	1.5	35.1	1.1	71.9	2.4	2.5	3 Jun	2.3	4808
EC		28 Apr	4.0	47.3	2.9	89.0	3.0	7.0	26 Jul	6.1	622
Yellow Bishop											
WC grids 3318 &3418	*	4 Dec	2.0	23.3	1.0	103.4	3.4	3.0	17 Mar	1.8	777

Table 4: Estimates of the primary moult parameters of individual primary feathers for adult widowbirds in South Africa

(a) White-winged Widow, Gauteng, n=685

Primary	Mean starting date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Standard error (days)	Mean completing date	Standard error (days)
1	21 Apr	2.7	29.0	2.4	5.0	1.5	26 Apr	2.7
2	20 Apr	2.6	28.2	2.2	8.8	1.9	29 Apr	2.7
3	24 Apr	2.5	25.7	2.1	8.1	1.8	2 May	2.5
4	27 Apr	2.5	25.0	2.1	7.3	1.8	4 May	2.5
5	30 Apr	2.3	22.4	1.8	11.6	2.1	12 May	2.4
6	8 May	2.2	19.9	1.7	7.7	1.8	16 May	2.2
7	16 May	2.2	17.6	1.8	5.2	1.5	21 May	2.1
8	20 May	2.1	17.6	1.9	5.7	1.5	26 May	2.0
9	23 May	2.5	23.2	2.0	13.0	2.3	5 Jun	2.5
mean					8.1			

(b) Red-collared Widow, Gauteng, n=667

Primary	Mean starting date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Standard error (days)	Mean completing date	Standard error (days)
1	6 Apr	3.1	39.9	2.9	16.0	2.4	22 Apr	2.9
2	6 Apr	3.0	38.6	2.7	17.9	2.5	24 Apr	2.9
3	10 Apr	2.9	37.0	2.6	17.5	2.5	27 Apr	2.9
4	19 Apr	2.7	34.0	2.4	14.4	2.2	3 May	2.7
5	28 Apr	2.6	31.4	2.3	9.4	1.8	7 May	2.6
6	2 May	2.4	27.3	2.0	12.9	2.1	15 May	2.4
7	10 May	2.2	24.9	2.0	10.7	1.9	21 May	2.3
8	15 May	2.1	21.8	1.8	13.6	2.1	28 May	2.2
9	18 May	1.9	19.4	1.6	17.1	2.2	4 Jun	2.1
mean					14.4			

(c) Fan-tailed Widow, KwaZulu-Natal grid 2930, n=1002

Primary	Mean starting date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Standard error (days)	Mean completing date	Standard error (days)
1	9 Apr	2.5	24.4	1.7	6.8	1.7	16 Apr	2.6
2	7 Apr	2.4	21.5	1.7	6.4	1.6	14 Apr	2.7
3	11 Apr	2.4	20.8	1.6	8.5	1.9	19 Apr	2.6
4	11 Apr	2.3	19.4	1.4	11.7	2.3	23 Apr	2.7
5	13 Apr	2.2	17.4	1.3	17.2	2.7	30 Apr	2.6
6	24 Apr	2.5	18.2	1.5	9.6	2.4	3 May	2.6
7	29 Apr	2.6	15.1	1.5	11.0	2.5	10 May	2.4
8	3 May	2.5	14.9	1.3	17.8	2.8	21 May	2.2
9	17 May	2.2	10.4	1.2	13.0	2.3	30 May	1.6
mean					11.3			

(d) Yellow Bishop, Western Cape grids 3318 and 3418, n=777

Primary	Mean starting date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Standard error (days)	Mean completing date	Standard error (days)
1	11 Dec	2.2	19.7	1.4	14.4	2.1	25 Dec	1.9
2	12 Dec	2.1	19.5	1.3	17.3	2.2	29 Dec	1.9
3	18 Dec	2.1	19.4	1.3	18.7	2.2	6 Jan	1.8
4	24 Dec	2.4	25.2	1.5	24.3	2.5	17 Jan	2.0
5	4 Jan	1.9	19.0	1.3	21.4	2.1	25 Jan	1.7
6	19 Jan	1.9	21.2	1.4	20.9	2.1	8 Feb	1.8
7	30 Jan	1.9	22.2	1.4	21.7	2.2	21 Feb	1.9
8	11 Feb	2.1	25.3	1.5	28.5	2.5	11 Mar	2.2
9	25 Feb	2.2	26.1	1.6	24.5	2.5	22 Mar	2.4
mean					21.3			

Table 5: Breeding and moult in *Euplectes* species in South Africa. Average incubation and nestling periods are in days (from Tarboton 2001). Median breeding month and start and end of moult are calculated from data in Tables 2 and 3
Localities are abbreviations for South African provinces: WC=Western Cape, KZN=KwaZulu-Natal, Tvl=former Transvaal

Species	Incubation	Nestling	Sum	Locality	Median breed (month)	Moult start (month)	Moult start – median breeding (month)	Breed end (month)	Moult start – end of breeding (month)
Red Bishop	13	14.5	27.5						
Yellow-crowned Bishop	12	11	23						
Yellow Bishop	13.5	14.5	28	SWC	9.6	12.1	2.5	11.2	0.9
Fan-tailed Bishop	12.5	15.5	28	KZN	12.4	4.1	3.7	2.5	1.6
White-winged Widow	12	12	24	Tvl	1.3	4.6	3.3	2.9	1.7
Red-collared Widow	14	16	30	Tvl	12.6	4.2	3.6	2.6	1.6
Long-tailed Widow	14	15	29	KZN	12.4	3.9	3.5	2.6	1.3
Long-tailed Widow				Tvl	12.9	3.9	3.0	2.8	1.1

Figure 1: Distributions, in southern Africa, of five *Euplectes* species which occur in South Africa, where darker shading indicates higher reporting rates (from Harrison *et al.* 1997); the final graphic shows the Grassland biome (from Allan *et al.* 1997)

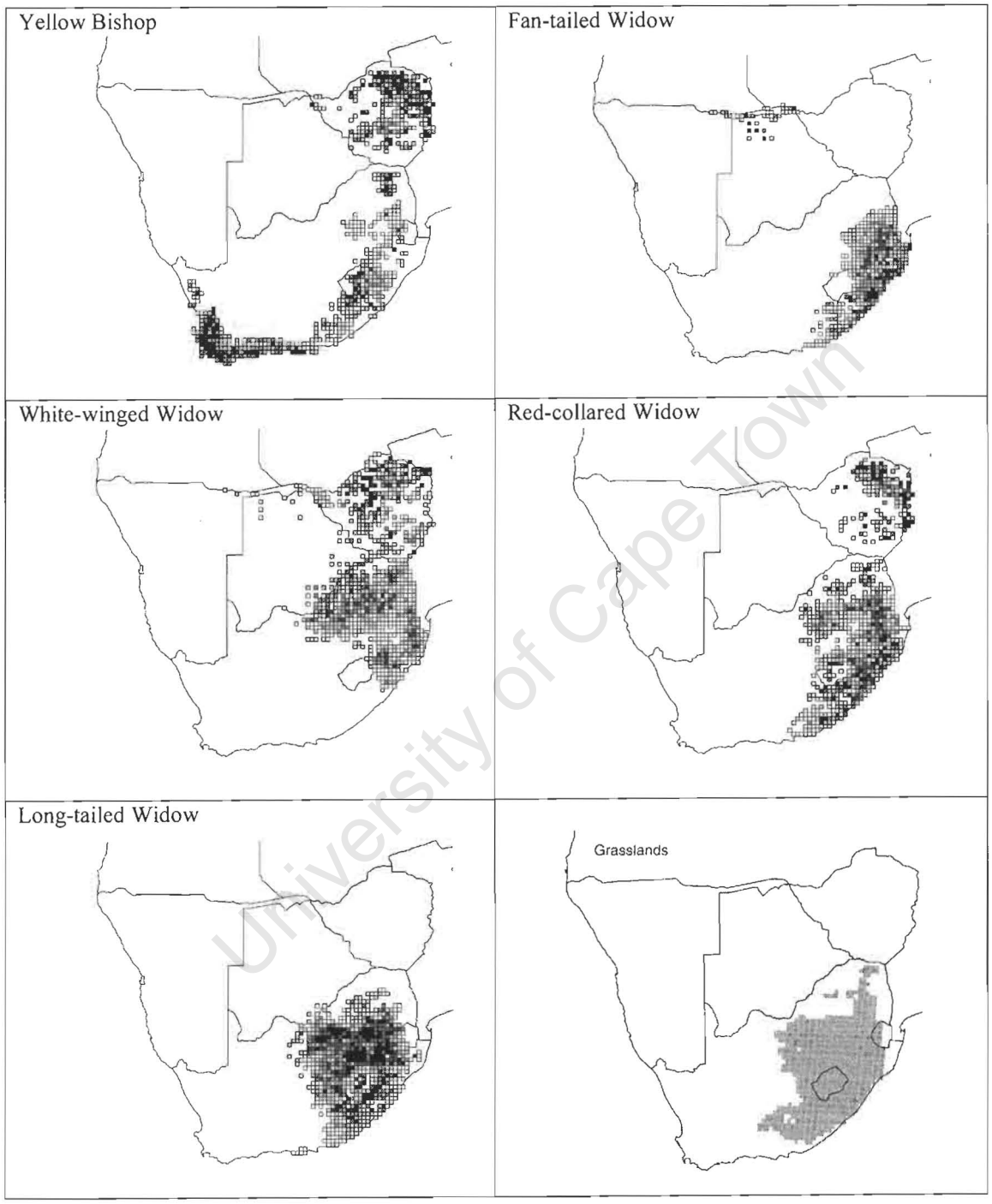


Figure 2: Capture sites for adult widowbirds in South Africa, showing sites from which primary moult data were obtained. Open circles in the Western Cape represent Yellow Bishop records; open circles in KwaZulu-Natal are for Fan-tailed Widow records; open circles in Gauteng are for White-winged Widow and Red-collared Widow records; closed squares are Long-tailed Widow records. For Southern Red Bishop capture sites, see Chapter 5

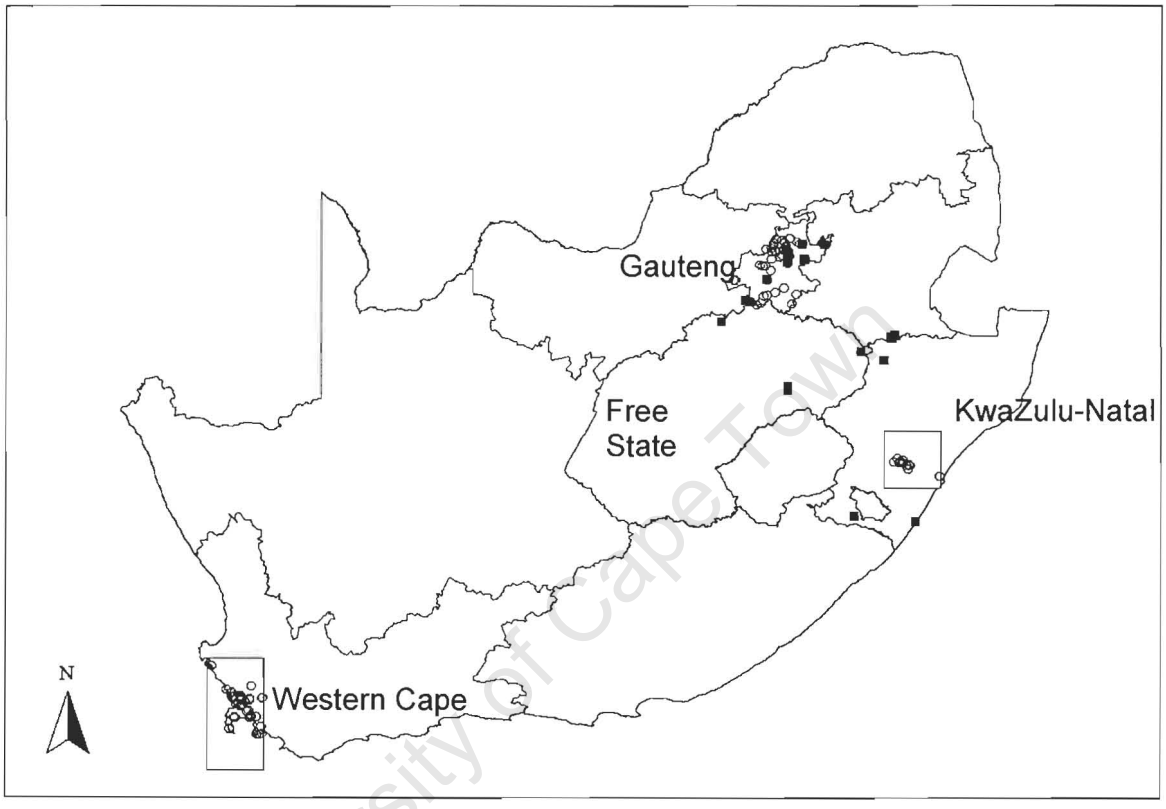


Figure 3: Relative feather masses for three adult *Euplectes* species in South Africa Southern Red Bishop, open triangles; White-winged Widow, crosses; Long-tailed Widow, solid squares

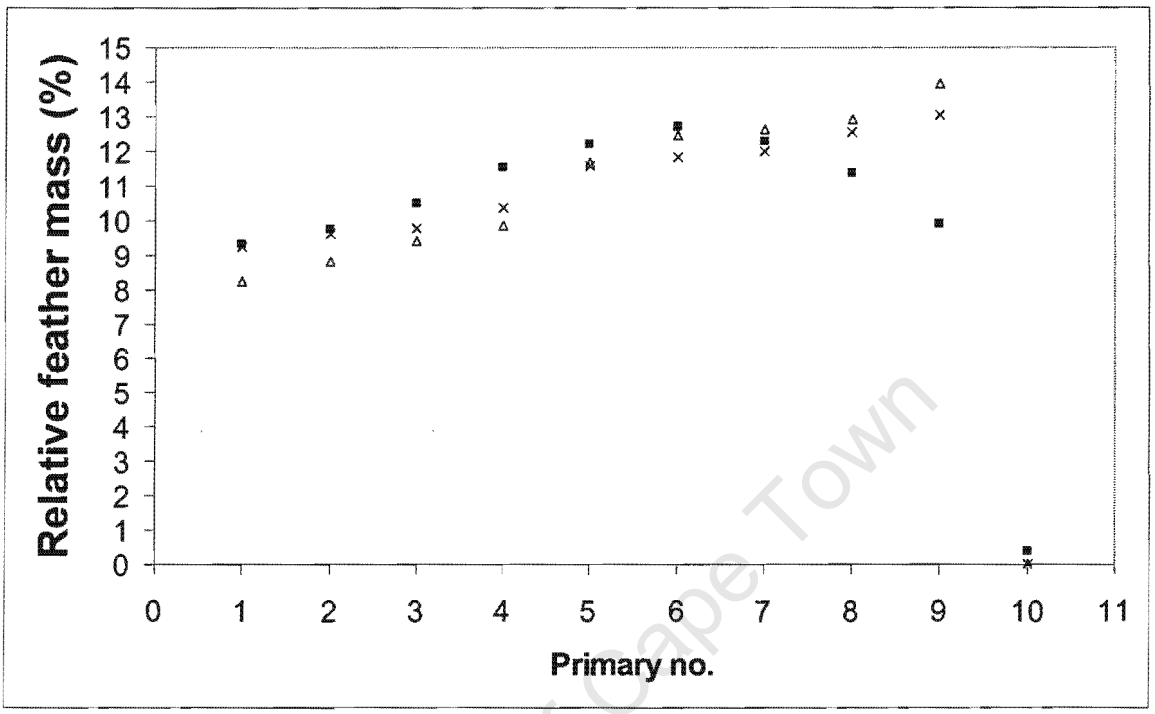
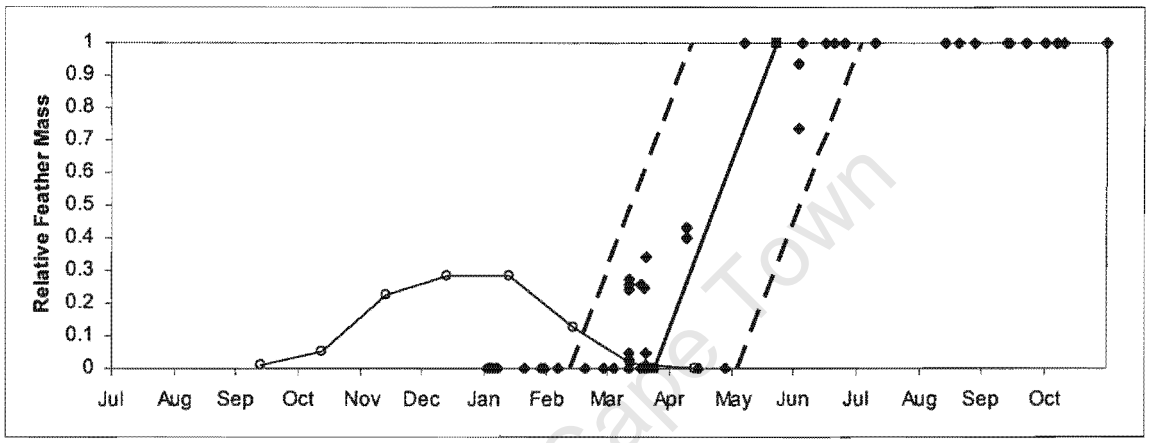
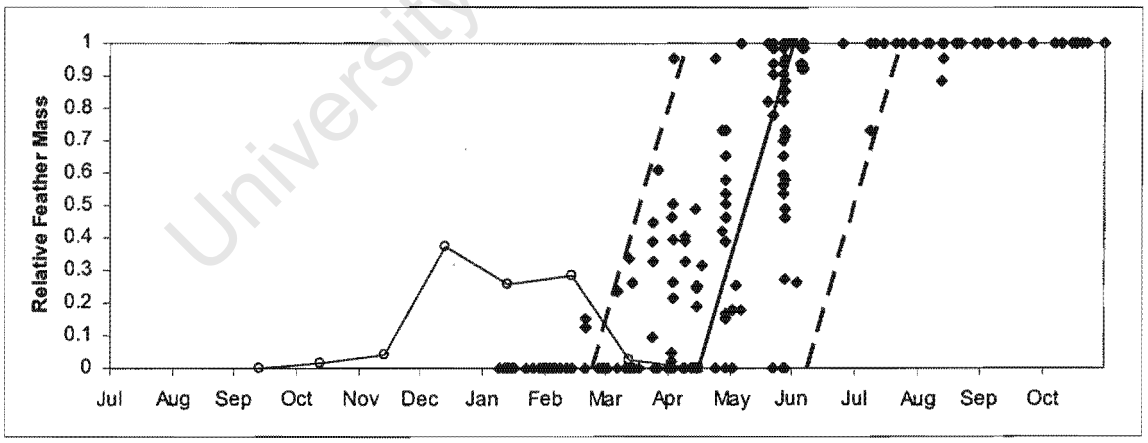


Figure 4: Timing of egg-laying and primary moult for adult *Euplectes* species in different parts of South Africa; the open circles with thin solid line shows the proportion of eggs laid per month (from the Nest Record Cards summary by Prŷs-Jones and Newton unpublished data); the solid diamonds represent relative feather mass values by date; the solid diagonal line joins the estimated mean start and end dates of moult, while the diagonal dotted lines show the approximate 95% confidence intervals of moult scores on any given date. For Southern Red Bishop graphs, see Chapter 5

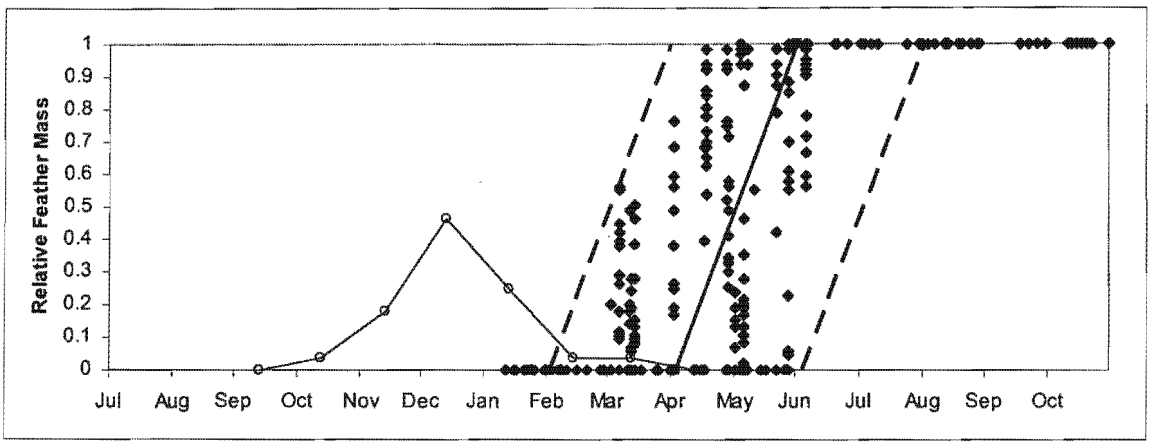
(a) Timing of breeding and primary moult in Long-tailed Widows, all records



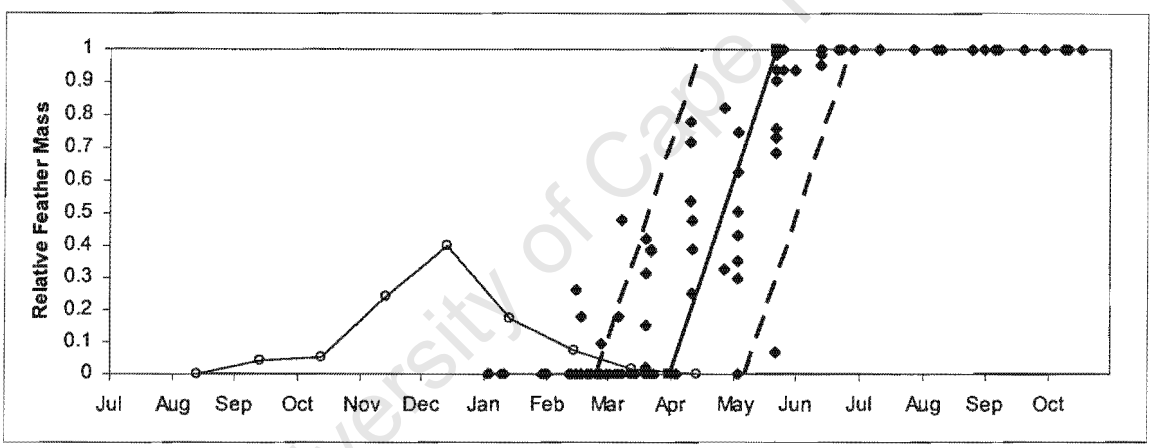
(b) Timing of breeding and primary moult in White-winged Widows, Gauteng (grids 2527, 2528, 2627, 2628)



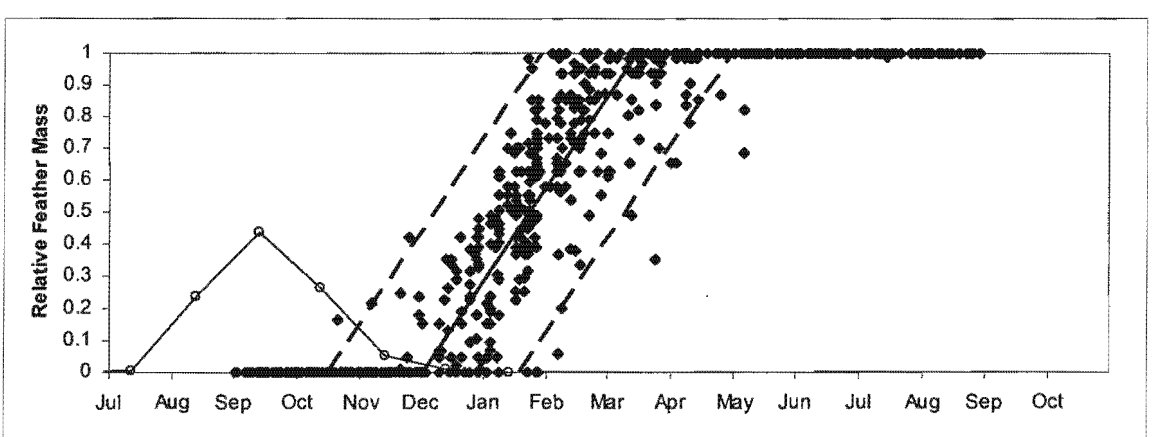
(c) Timing of breeding and primary moult in Red-collared Widows, Gauteng (grids 2527, 2528, 2627, 2628), using relative feather masses of White-winged Widow



(d) Timing of breeding and primary moult in Fan-tailed Widows, grid 2930 (KwaZulu-Natal), using relative feather masses of White-winged Widow



(e) Timing of breeding and primary moult in Yellow Bishops, Western Cape (grids 3318-3418), using relative feather masses of White-winged Widow



Chapter 7

Breeding seasonality and primary moult in weavers in eastern South Africa

Breeding seasonality and primary moult in weavers in eastern South Africa

Abstract

The breeding seasonality of Village *Ploceus cucullatus*, Yellow *P. subaureus*, Spectacled *P. ocularis* and Thick-billed Weavers *Amblyospiza albifrons* in KwaZulu-Natal is fairly similar. The three *Ploceus* species have the medians of their breeding periods in November and that of the Thick-billed Weaver is in December. The length of the egg-laying season is 3.7–4.1 months in the three *Ploceus* species and 4.4 months in the Thick-billed Weaver. The breeding seasonality is similar in the Eastern Cape and former Transvaal regions, both also being summer rainfall areas, but with some more variability than in KwaZulu-Natal. In the three *Ploceus* species, duration of moult was shortest in Yellow Weavers (66 days), intermediate in Village Weavers (96 days), and longest in Spectacled Weavers (114 days). Primary moult started in February and ended in May for all three species in KwaZulu-Natal. There were enough data for Village Weaver to analyse moult for three separate years, imposing a constant duration on all years. Start date varied significantly by up to two weeks in different years. The Thick-billed Weaver had a similar duration of moult in Gauteng and KwaZulu-Natal of 71 and 73 days respectively, but the start date was significantly earlier in Gauteng (five weeks earlier).

Introduction

The Village *Ploceus cucullatus*, Yellow *P. subaureus*, Spectacled *P. ocularis* and Thick-billed Weavers *Amblyospiza albifrons* are four common ploceids found in eastern South Africa. They have broadly similar distributions in the littoral regions of the Eastern Cape and KwaZulu-Natal, with the Yellow Weaver being the most coastal (Harrison *et al.* 1997). Farther north, the distributions diverge (Harrison *et al.* 1997, Parker 1999, Fry and Keith 2004). In southern Africa these species are confined to the summer rainfall region.

The four species are poorly studied in southern Africa, although there is an extensive literature on the Village Weaver farther north in Africa (e.g. Collias and

Collias 1970, Camara-Smeets 1982, Adegoke 1983, Lahti and Lahti 2002). Even though the Thick-billed Weaver has a vast distribution extending northwards to East and West Africa, the only comprehensive studies are at the southern extremity of its range, in KwaZulu-Natal (Laycock 1979, 1982, 1984). The Spectacled Weaver is also a widespread African species but with even fewer studies (Skead 1953, Craig 1984). Limited field notes have been published for Yellow Weaver (Skead 1995).

The Spectacled Weaver is mainly insectivorous; it is a solitary, monogamous breeder (Craig 1984). The other three ploceids are largely seed-eaters; they are colonial, polygynous breeders (Fry and Keith 2004). The peak breeding season in KwaZulu-Natal for these four weavers is September to January (Harrison *et al.* 1997).

Of the four species, only the Thick-billed Weaver has undergone a range expansion (Harrison *et al.* 1997); it expanded its range to Gauteng in the 1960s, in what appears to have been a natural expansion along the Olifants River from Mpumalanga (Tarboton 1968, Leinberger 1982, Winterton 1982, Tarboton *et al.* 1987, Harrison *et al.* 1997). This range expansion is continuing (Leinberger 1997). This region has summer rainfall as does KwaZulu-Natal. There have been no studies of this species in Gauteng.

The aim of this paper was to extend the range of species for which estimates of primary moult parameters are available. This paper examines the parameters of primary moult of adults of these four species in eastern South Africa, and considers the timing of moult in relation to timing of breeding. In KwaZulu-Natal, adult wing-moult has been considered in Thick-billed Weavers; but this study used an unorthodox approach, so the results are not readily compatible with any other studies (Laycock 1982, Brown *et al.* 2001). Wing-moult has been studied in Village Weavers in the Eastern Cape, using the same analysis technique as used in this paper, so the results are comparable (Craig *et al.* 2001). In addition to presenting results on primary moult for the four species in KwaZulu-Natal, this paper presents results for the Thick-billed Weaver in the new extension of its range in Gauteng.

Methods

Breeding seasonality data were obtained from the BirdLife South Africa Nest Record Card Scheme (NRC) (RP Prŷs-Jones and I Newton unpublished data; Underhill *et al.*

1991) and by adding my own unpublished records of breeding of Thick-billed Weaver in Gauteng. Prŷs-Jones and Newton (unpublished data) estimated the month of laying of the first egg for each record. They then summarised breeding seasonality for all birds in South Africa by presenting monthly totals of clutches laid per species per region. One of the regions they used was the former Transvaal province: this region incorporates the current Gauteng Province, from where most of the records originate. To compare breeding seasonality of weavers, the tabulated data of Prŷs-Jones and Newton (unpublished data) were used to estimate the median and the 5th and 95th percentiles for each species and region. The median was calculated by finding the cumulative monthly sums of the percentage of nest records. The median month was the month in which the cumulative sum first exceeded 50%. The values of the sums of the previous and successive months were used to assign a relative distance into the month. For example, if there were 47% of cumulative records by the end of October, and 64% by the end of November, the median clearly is during November. Then using proportions gives (50–47)/(64–47) = 17.7%, the relative distance into November. Thus the median lies 17.7% into November (month 11), calculated as 11.177 (and rounded to 11.2 for presentation). The 5th and 95th percentiles were interpolated in a similar fashion. Dates in January were recorded as being in month 1 (not month 0).

Ringing data were collected by ringers in the standard SAFRING (South African Bird Ringing Unit) electronic format. This includes standard ringing information (such as location and date) and data on bird body mass, wing length and primary moult (de Beer *et al.* 2001). Ringing and recapture records submitted to SAFRING until mid-January 2005 for adults of the four species were extracted from the database. Primary moult records were extracted from SAFRING's database for Village, Yellow, Spectacled and Thick-billed Weavers in KwaZulu-Natal and for Thick-billed Weavers in Gauteng (Figure 1). The Village Weaver records were restricted to a one-by-one degree grid cell with 29°S and 30°E in the north-western corner. In all species moult of the primaries is ascendant, with the feathers renewed from innermost to outermost.

To determine the relative mass of each primary, as described in Underhill and Summers (1993), the primaries of the wings of a Thick-billed Weaver specimen were dried in an oven at 60°C for 24 hours to eliminate moisture and weighed (Ohaus GA200D balance, precision 0.0001g). These values were averaged and used for to calculate the relative mass of each primary. For Village Weaver the published relative

mass of each primary was used (Craig *et al.* 2001). Wings of Yellow and Spectacled Weavers were not available. Underhill and Joubert (1995) showed that small samples are adequate to determine the relative masses of primary feathers because there is little intra-specific variation in this characteristic; they also showed that within the Charadriiformes, the relative masses of the primary feathers were so similar that the average value for the species for which data were available could safely be used for species for which data were unavailable, and we used the same approach here. The wing shape of the Yellow Weaver is most similar to that of the Cape Weaver (HDO pers. obs) and the published relative masses for this species were used (Underhill and Joubert 1995). For Spectacled Weaver the wing shape is partially described by Moreau (1960: 449) and the most similar wing is that of the Thick-billed Weaver (pers. obs).

The Underhill-Zucchini moult model (Underhill and Zucchini 1988), developed to estimate start and duration of primary moult, was applied to the data sets. The data were considered to be of 'type 2' of Underhill and Zucchini (1988), because full moult scores were recorded for each bird and all birds were considered available for sampling throughout the moult period. The parameters of primary moult were estimated using the transformations recommended by Summers *et al.* (1980, 1983), designed to reduce the bias introduced by the fact that the individual feathers are of different masses. The moult index used was percentage feather mass grown (PFMG), calculated from the moult score for the individual feathers according to the method of Underhill and Summers (1993).

Brandao (1998) (see also Underhill *et al.* in press) extended the Underhill-Zucchini (1988) moult model to estimate starting dates for groups of birds (e.g. males and females, or annual groups), holding the other two parameters (duration and standard deviation) constant. She also developed rigorous statistical testing, using the likelihood ratio test, of the null hypothesis that the starting date for each group was the same. This method was applied to estimate starting dates for Village Weavers for each of three years.

Results

In KwaZulu-Natal, breeding seasonality by the four species of weavers is fairly similar; the three *Ploceus* species have the medians of their breeding periods in

November and that of the Thick-billed Weaver is in December (Table 1). The length of the egg-laying season (5th and 95th percentiles) is 3.7–4.1 months in the three *Ploceus* species and 4.4 months in the Thick-billed Weaver. The breeding seasonality is similar in the Eastern Cape and former Transvaal regions, both also being summer rainfall areas, but with some more variability than in KwaZulu-Natal (Table 1).

Moulting birds were captured throughout the moulting season (Figure 2); this enables the moult parameters to be estimated reliably. For Thick-billed Weavers, however, the number of records of active moult is relatively small (60 of 179 records in Gauteng, and 105 of 462 records in KwaZulu-Natal); this is reflected in the larger standard errors compared to the other species (Table 3).

In the three *Ploceus* species duration of moult was shortest in Yellow Weaver (66 days), intermediate in Village (96 days), and longest in Spectacled Weavers (114 days). Moult started in February and ended in May for these three species in KwaZulu-Natal.

There were sufficient data for Village Weaver to analyse moult for three separate years, imposing a constant duration and standard deviation on all years. This is valid because there was no significant difference when using individual durations per year (likelihood ratio test, $\chi^2_3=3.58$, $p>0.05$). Start date varied by up to two weeks in different years (Table 3). These differences were highly significant (likelihood ratio test, $\chi^2_3=173.8$, $p<0.001$).

The Thick-billed Weaver had a similar duration of moult in Gauteng and KwaZulu-Natal of 2.4 months, but the start date was five weeks earlier in Gauteng. The difference in start date was highly significant (likelihood ratio test, $\chi^2_2=77.9$, $p<0.001$).

Discussion

Breeding in the summer rainfall region for these four weavers starts in September or October, and ends in January or February. This corresponds well with the published peak breeding season in KwaZulu-Natal of September to January (Harrison *et al.* 1997).

Moult has not been analysed for Yellow and Spectacled Weavers previously (Craig 1983), although Britton and Britton (1986) published a figure with eight moult records for Spectacled Weavers in Mombasa, Kenya. The duration of primary moult

for Village Weavers was estimated to be 109 days, from 17 February to 5 June, in the Eastern Cape (Craig *et al.* 2001); in KwaZulu-Natal primary moult started an average of five days earlier and lasted two weeks less (Table 3).

Moult in Thick-billed Weavers has been studied in KwaZulu-Natal by estimating duration of moult visually from plots of moult score versus date. Laycock (1982) found moult in the population from December to June; this includes secondary moult which finishes a little later than primary moult. Brown *et al.* (2001) found primary moult from April to June. The present analysis gives a shorter duration of moult (2.4 months). Laycock (1982) found no difference in moult timing and duration in males and females.

No studies of Thick-billed Weavers in Gauteng exist; there are only published sightings showing that the species has expanded its range to this province (Harrison *et al.* 1997). This study shows breeding and moulting starting five weeks earlier in Gauteng compared to KwaZulu-Natal. We cannot offer an explanation for this unexpected result, and this clearly represents an opportunity for detailed study. The result obtained does not parallel that for the Southern Masked Weaver which has also expanded its range, into the Western Cape (chapter 5).

The monogamous species, Spectacled Weaver, has a similar peak breeding season (November) to the two polygynous *Ploceus* species, Yellow and Village Weavers. Primary moult in the Spectacled Weaver starts 1–3 weeks earlier, and ends 1–3 weeks later, than the other two species. Moult follows soon after breeding in all three species as is normal in passerines (Payne 1972). These weavers have a well-defined breeding and moulting season, which seems to be related to the mesic environment rather than mating system.

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Table 1: Months of egg-laying (percentages) for Village Weaver, Spectacled Masked Weaver, Yellow Weaver and Thick-billed Weaver in South Africa (from Prŷs-Jones and Newton unpublished data). For Thick-billed Weaver in the former Transvaal, HDO's records from Gauteng have been included. The percentages are summarized as 5th percentile (represents start of moult), 95th percentiles (end of moult), range (90% range of months of egg-laying) and median egg-laying month; numbers represent parts of months, e.g. 12.5 = mid December, 1.4 = 40% through January (see text)
Localities are abbreviations for South African provinces: EC=Eastern Cape, KZN=KwaZulu-Natal, Tvl=former Transvaal (this region incorporates the current Gauteng Province)

Species	Area	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	n	5th	95th	Range	Median
Spectacled Weaver																		
	EC			6	32	35	21	6						34	9.9	1.2	3.3	11.3
	KZN			9	18	32	34	7						56	9.6	1.3	3.7	11.7
	Tvl				20	40	40							5	10.3	12.9	2.6	11.8
Yellow Weaver																		
	EC			17	29	25	4	25						24	9.3	1.8	4.5	11.2
	KZN			18	23	38	13	7	<1					267	9.3	1.4	4.1	11.2
Village Weaver																		
	EC				20	10	50	20						10	10.3	1.8	3.5	12.4
	KZN			15	3	39	34	9						98	9.3	1.5	4.1	11.8
	Tvl		7	40	16	24	9	2	2					55	8.7	12.9	4.2	10.2
Thick-billed Weaver																		
	EC			5	5	14	64	9	5					22	10.1	2.0	3.9	12.4
	KZN		1	2	10	13	39	23	13					101	10.2	2.6	4.4	12.6
	Tvl		10	20	10	20	20	20						10	9.5	1.8	4.3	11.5

Table 2: Individual primary feather masses (g) of a Thick-billed Weaver specimen from Durban, KwaZulu-Natal, and the mean relative mass of each primary, used in the calculation of Percentage Feather Mass Grown

Primary	Feather mass (g)		Mean relative feather masses
	Left wing	Right wing	
1	0.0239	0.0205	9.5
2	0.0266	0.0212	10.2
3	0.0258	0.0223	10.3
4	0.0267	0.0240	10.9
5	0.0298	0.0258	11.9
6	0.0305	0.0267	12.3
7	0.0285	0.0265	11.8
8	0.0271	0.0239	11.0
9	0.0248	0.0223	10.1
10	0.0047	0.0042	1.9
Total	0.2484	0.2174	100.0

Table 3: Estimates of the primary moult parameters of adult Village, Yellow, Spectacled and Thick-billed Weavers in KwaZulu-Natal and Gauteng, South Africa
Localities are abbreviations for South African provinces: KZN=KwaZulu-Natal, GP=Gauteng Province, EC = Eastern Cape

Locality /year	Mean starting date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Duration (months)	Standard error (days)	Mean completion date	Standard error (days)	n
Spectacled Weaver										
KZN	3 Feb	3.4	21.0	1.3	114.1	3.8	4.3	28 May	2.3	388
Yellow Weaver										
KZN	27 Feb	2.6	19.7	1.4	65.8	2.2	3.9	4 May	2.8	653
Village Weaver, in the one degree grid cell with 29°S 30°E in the north western corner										
KZN	12 Feb	2.4	28.5	1.1	96.1	3.2	3.4	19 May	2.1	1215
2001	2 Feb	4.7	31.5	1.6	106.1	3.5	4.9	18 May	4.2	673
2002	7 Feb	4.0	31.5	1.6	106.1	3.5	4.9	24 May	3.8	673
2003	14 Feb	5.5	31.5	1.6	106.1	3.5	4.9	31 May	8.7	673
Village Weaver, Craig *et al.* (2001)										
EC	17 Feb	5	40.1	2.4	109	3.6	6	5 Jun	3.7	436
Thick-billed Weaver										
GP	20 Feb	4.3	23.8	2.6	71.2	2.4	6.8	2 May	5.4	179
KZ	26 Mar	3.9	22.9	2.2	73.3	2.4	6.4	8 Jun	5.2	462

Figure 1: Capture sites for adult Village, Yellow, Spectacled and Thick-billed Weavers in eastern South Africa, from which primary moult data were obtained. Gauteng shows Thick-billed Weaver records; the square in KwaZulu-Natal shows the records for Village Weavers; the whole KwaZulu-Natal has records for Yellow, Spectacled and Thick-billed Weavers, largely in the square

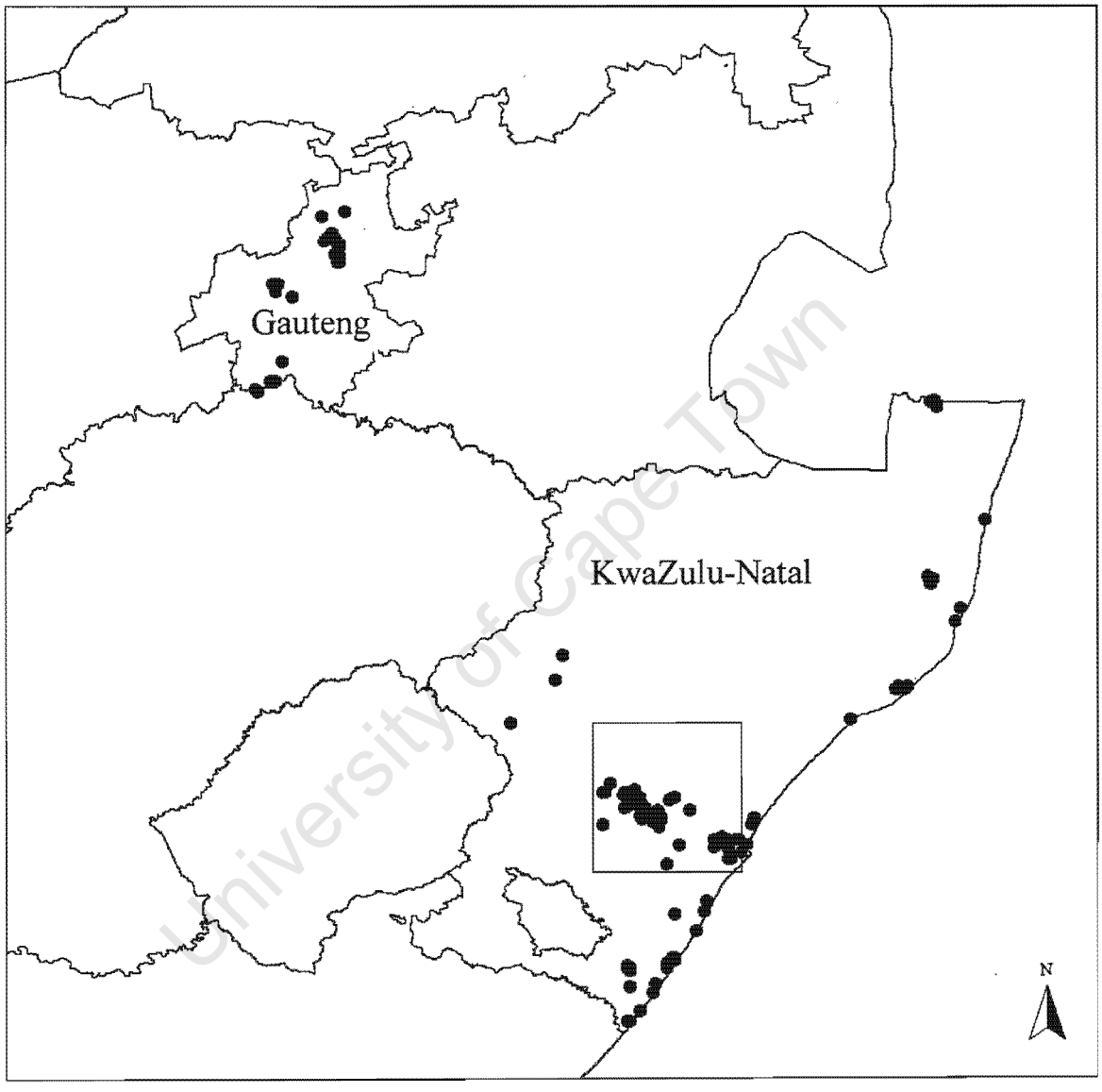
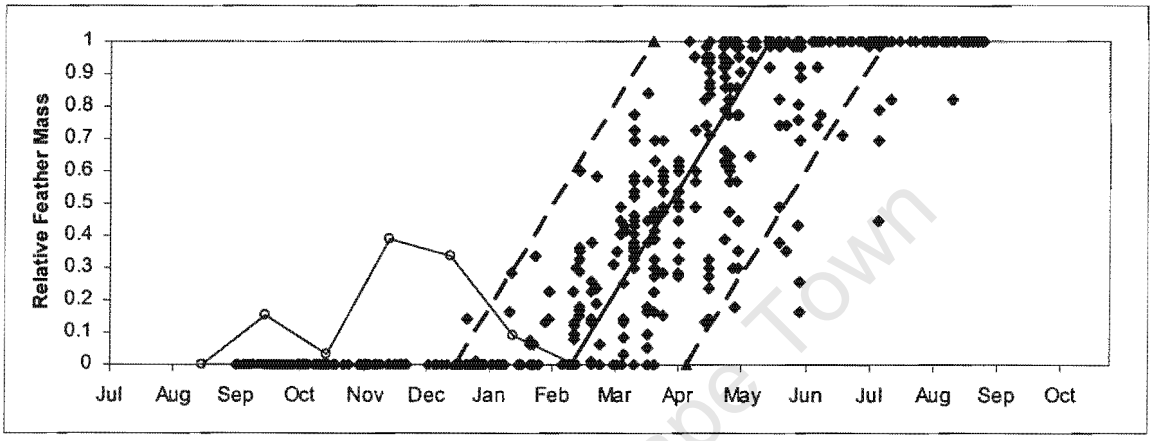
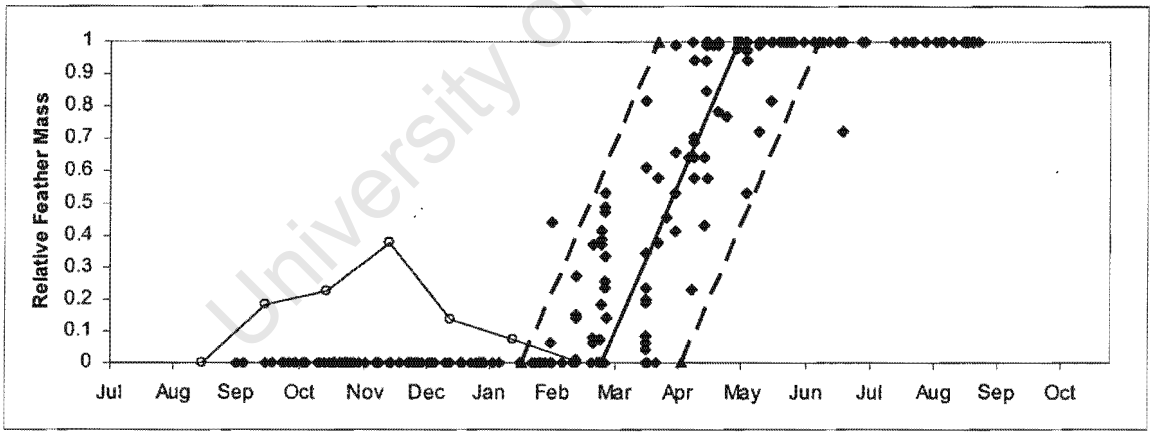


Figure 2: Timing of egg-laying and primary moult for adult weavers in different parts of South Africa; the open circles with thin solid line shows the proportion of eggs laid per month (from the Nest Record Cards summary by Prŷs-Jones and Newton unpublished data); the solid diamonds represent relative feather mass values by date; the solid diagonal line joins the estimated mean start and end dates of moult, while the diagonal dotted lines show the approximate 95% confidence intervals of moult scores on any given date

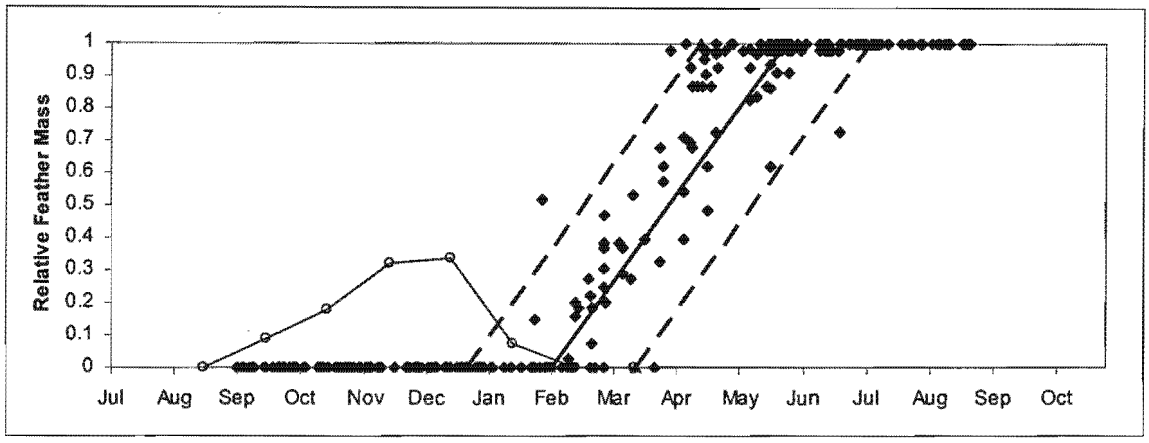
(a) Village Weaver, grid 2930 in KwaZulu-Natal



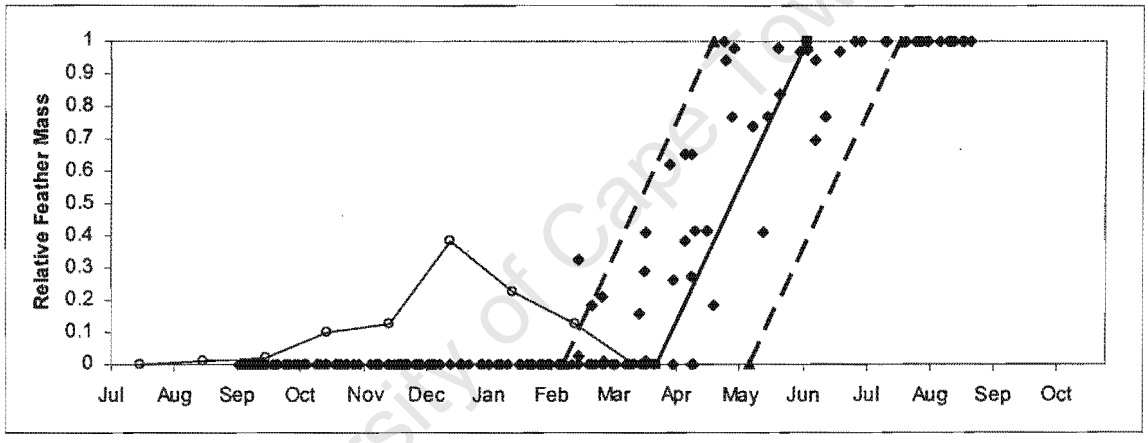
(b) Yellow Weaver, KwaZulu-Natal



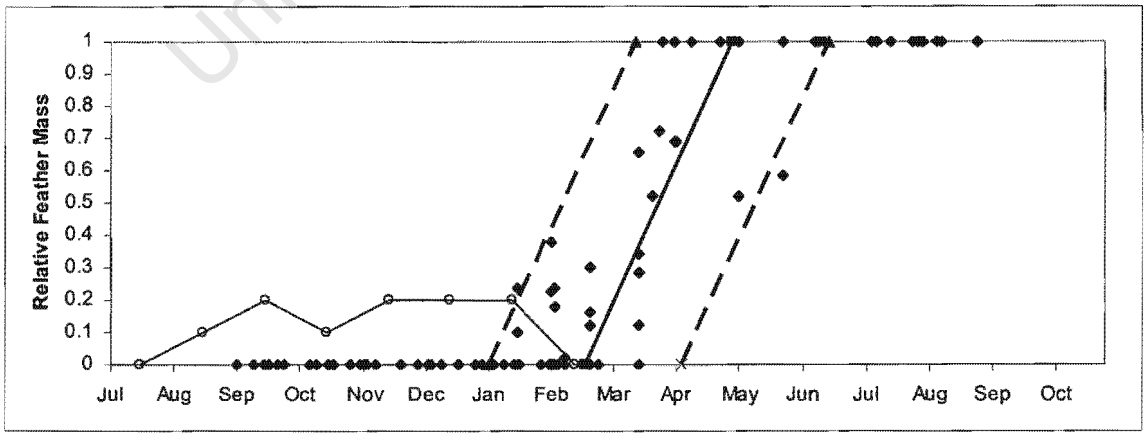
(c) Spectacled Weaver, KwaZulu-Natal



(d) Thick-billed Weaver, KwaZulu-Natal

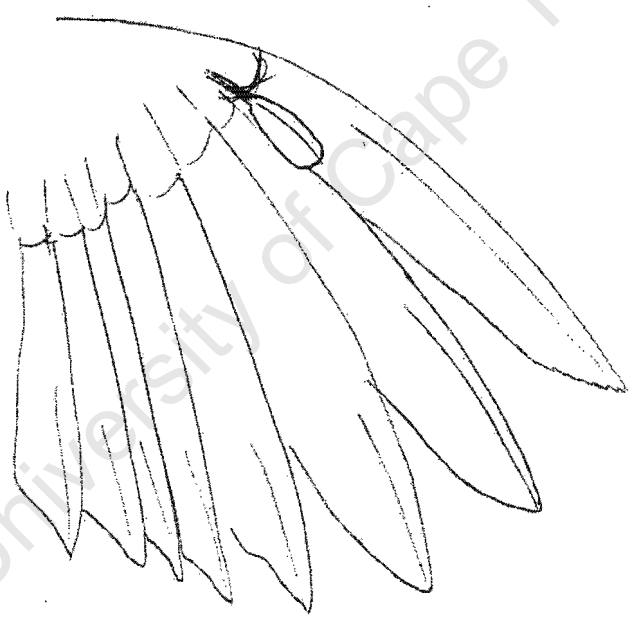


(e) Thick-billed Weaver, Gauteng



Chapter 8

Annual variation in primary moult parameters in Cape Weavers, Southern Masked Weavers and Southern Red Bishops in the Western Cape, South Africa



Annual variation in primary moult parameters in Cape Weavers, Southern Masked Weavers and Southern Red Bishops in the Western Cape, South Africa

Abstract

Duration of primary moult was similar in Cape Weavers and Southern Red Bishops (96 days) and slightly shorter in Southern Masked Weavers (75 days) over 11 years in the Western Cape. Mean start date of moult averaged over 11 years was earliest in Cape Weavers (12 November), intermediate in Southern Red Bishops (5 December) and latest in Southern Masked Weaver (14 January). The difference between earliest and latest starting dates for different years was greatest for Southern Red Bishops (35 days), intermediate in Cape Weavers (31 days) and least for Southern Masked Weavers (21 days). This variation in start dates was due to variability in timing of rainfall in different years. End of moult followed after breeding which was correlated with the end of the rainy season. In a model of dry periods following the rainy season and peak breeding, Cape Weavers started primary moult an average of 29.2 days after the first dry period in October. Similarly Southern Red Bishops started moult 58.8 days after the first dry period in October. Southern Red Bishops seemed to continue breeding for longer than Cape Weavers after the first dry period after October. A possible reason for this ability to breed for longer may be that Southern Red Bishop chicks were less dependent on insects than were Cape Weaver chicks. The Southern Masked Weaver, however, showed the onset of moult as late January in earlier years, and then stabilized around 6 January. Thus onset of moult in different years in the Southern Masked Weaver appears to have advanced over time. Timing of breeding in this species is predicted to advance in the future, and this could mean an advance in timing of moult.

Introduction

Annual variation in moult parameters has been poorly documented, especially in the southern hemisphere. There are several published studies in the northern hemisphere (Cassin's Auklet *Ptychoramphus aleuticus,* Emslie *et al.* 1990; Curlew Sandpiper

Calidris ferruginea, Figuerola and Bertolero 1995; Dunnock *Prunella modularis,* Ginn 1975; Reed Bunting *Emberiza schoeniclus,* Sondell 2000; Pied Flycatcher *Ficedula hypoleuca,* Siikamaki *et al.* 1994; Bullfinch *Pyrrhula pyrrhula,* Newton 1966, 1999; Lesser Redpoll *Carduelis flammea,* Evans 1966; Mountain White-crowned Sparrow *Zonotrichia leucophrys* Morton and Morton 1990).

The Southern Masked Weaver *Ploceus velatus,* Cape Weaver *P. capensis* and Southern Red Bishop *Euplectes orix* are three common ploceids in the Western Cape, South Africa. They are polygynous, colonial, seed-eating weavers. Cape and Southern Masked Weavers breed mainly in trees or reeds; Southern Red Bishops breed chiefly in reeds (Fry and Keith 2004). The Southern Masked Weaver is a relatively new arrival in the Western Cape, having expanded its range into this region since the 1940s (Oschadleus *et al.* 2000 and references therein; see also Chapter 5).

In the Western Cape the Cape Weaver breeds from August to November, the Southern Red Bishop from August to early December (Craig *et al.* 2001), and the Southern Masked Weaver from September to November (Oschadleus *et al.* 2000; Chapter 5).

In the Western Cape adult wing-moult is known to be from October to March in Cape Weavers, November to April in Southern Red Bishops, and January to March in Southern Masked Weavers (Oschadleus *et al.* 2000, Craig *et al.* 2001; Chapter 5). In these species moult of the primaries is ascendant, with the feathers renewed from innermost to outermost. This paper investigates inter-year variation in the timing of primary moult for these three species over an 11-year period in the Western Cape.

Methods

Ringing data were collected by ringers in the standard SAFRING (South African Bird Ringing Unit) electronic format. This includes standard ringing information (such as location and date) and data on bird body mass, wing length and primary moult (de Beer *et al.* 2001). Primary moult records were extracted from the SAFRING database for Cape Weavers, Southern Red Bishops and Southern Masked Weavers in the one-degree area, 33°–34°S 18°–19°E, for the 11 years from 1 September 1993 to 1 September 2004 (Figure 1). The sites with the most ringing data were Goedeontmoeting farm (33°41'S 18°36'E), Rocklands farm (33°43'S 18°45'E),

Protea Hills (33°51'S 18°37'E), and gardens in Durbanville, a suburban area (33°51'S 18°38'E). The closest weather station to these sites is at Altydgedacht (33°50'S 18°38'E) and daily rainfall data were obtained from this station for the period 1993 to 2003.

The relative mass of each primary (as described in Underhill and Summers 1993) was obtained from published sources: Cape Weaver (Underhill and Joubert 1995), Southern Masked Weaver (Oschadleus *et al.* 2000) and Southern Red Bishop (Craig *et al.* 2001). For the first two species 10 primaries were used even though the 10th primary is small; for Southern Red Bishops nine primaries were weighed because the 10th is less than 0.001 g (pers. obs). The Underhill-Zucchini moult model (Underhill and Zucchini 1988), developed to estimate start and duration of primary moult, was applied to the data sets. The data were considered to be of 'type 2' of Underhill and Zucchini (1988), because full moult scores were recorded for each bird and all birds were considered available for sampling throughout the moult period. The parameters of primary moult were estimated using the transformations recommended by Summers *et al.* (1980, 1983), designed to reduce the bias introduced by the fact that the individual feathers are of different masses. The moult index used was percentage feather mass grown (PFMG), calculated from the moult score for the individual feathers according to the method of Underhill and Summers (1993).

Brandao (1998) (see also Underhill *et al.* in press) extended the Underhill-Zucchini (1988) moult model to estimate starting dates for groups of birds (e.g. males and females, or annual groups), holding the other two parameters (duration and standard deviation) the same for all groups. This method was applied to estimate starting dates for three weaver species over 11 years.

The starting date of moult was related to variables derived from the daily rainfall data. In the Western Cape, breeding occurs in the mid to latter part of the winter period during which the bulk of the region's rainfall occurs. However, the timing of this rainfall is variable between years. Because moult occurs after the end of the breeding season, I sought to explore a relationship between the end of the rainy season each year and the timing of moult. If such a relationship existed, it would also indicate that the end of the breeding season is related to the end of the rainy season.

The daily rainfall data were used to set up a daily index of wetness, based on the principle of exponential decay, to simulate the effect of cumulative rainfall.

Putting r_i as the rainfall (mm) on day i, the index of wetness W_i (which has units mm) for day i was computed as

$$W_i = 0.8\ W_{i-1} + r_i$$

Thus the effect of rainfall steadily decays through time. The index of wetness was started each year on 1 January, eliminating any possibility of start up effects in the rainfall index in October and November, the months for which the index was used. A simple strategy was proposed for the cessation of breeding for Cape Weavers and Southern Red Bishops: remain in breeding condition until the beginning of October; cease breeding (and prepare to moult) when conditions become dry. This strategy was operationalised by determining, for each year, the first day after 1 October on which the index of wetness dropped below 2 mm and using this as an explanatory variable to predict the estimated date of start of moult in a regression model. Other explanatory variables based on the rainfall were also considered: the total rainfall during the period 1 May to 30 September, and the date on which the cumulative rainfall for this period reached its median for the year.

Results

Over the 11-year study period 10468 weavers of the three species were captured within the grid 33°S 18°E (Figure 1), providing a large data set to study annual variation in moult parameters. Birds were captured throughout the moult season; this enabled the moult parameters to be estimated reliably. Moult parameters were calculated for the overall time period 1993–2003 (Table 1) and for each of these 11 individual years (Table 2).

For all years combined, the duration of primary moult was similar for Cape Weavers and Southern Red Bishops (96 days) and slightly shorter in Southern Masked Weavers (75 days). Mean start date of moult was earliest in Cape Weavers (12 November), intermediate in Southern Red Bishops (5 December) and latest in Southern Masked Weaver (14 January).

To calculate annual variation in start date of moult, the Brandao extension to the Underhill-Zucchini moult model was used. Over the 11 years, the estimated mean starting date of Cape Weaver primary moult lay between 27 October and 27

November, Southern Red Bishops between 27 November and 1 January, and Southern Masked Weavers between 4 and 25 January (Table 2, Figure 2). There were insufficient data for the algorithm to converge for Southern Masked Weavers in 1997. The difference between earliest and latest starting dates for different years was greatest for Southern Red Bishops (35 days), intermediate in Cape Weavers (31 days) and least for Southern Masked Weavers (21 days) (Table 1).

A striking aspect of the results was the parallelism between mean starting dates of primary moult of Cape Weavers and Southern Red Bishops in Figure 2; both showed similar pattern of starting dates for moult over 11 years (Figure 2). Cape Weavers started moult on average 28 days (s.d. 5 days) earlier than Southern Red Bishops; this lag was the least in 2003 (22 days) and greatest in 1993 (36 days). Plotting the onset of moult for these two species gives a correlation of 0.66 (Figure 3). For the Southern Masked Weaver, the onset of moult was relatively late from 1993 to 1995, and stabilized around 6 January for the period 1998 to 2003 (Figure 2).

Cape Weavers started primary moult an average of 30 days (s.d. 6 days, range 21–41) after the first dry period after the start of October, defined as the first day after 1 October on which the wetness index was below 2 mm. For Southern Red Bishops, the average delay was 59 days (s.d. 5 days). The regression model to predict the starting date of moult of Cape Weavers (y, days after 1 October) from the date on which the wetness index fell below 2 mm (t, days after 1 October) was $y=33.5 + 0.73t$ ($r^2 = 0.61$, d.f.=8, P=0.008). Similarly, the analogous regression model for Southern Red Bishops was $y=61.0 + 0.82t$ ($r^2 = 0.74$, d.f.=8, P=0.001).

This model is illustrated for three representative years (Figure 4). There was little rainfall in September 1993, probably resulting in little breeding (Figure 4a); both Cape Weavers and Southern Red Bishops started moult early (on 27 October and 2 December, respectively, Table 2). 1996 was a year with rain through the winter and spring without a dry period (Figure 4b), resulting in a late start to moult (27 November and 1 January, respectively). In 1998 there was little rain in September and October, resulting in an early start in moult (4 November and 8 December, respectively); the relatively large amount of rainfall at the start of November (Figure 4c) was too late for the continuation of breeding and failed to delay the onset of moult.

Other explanatory variables were considered, e.g. total rainfall during the period 1 May to 30 September, but were found to be uncorrelated with the date of

start of moult in both Cape Weavers and Southern Red Bishops. Similarly, there was no significant relationship between any of the rainfall variables and the onset of moult of Southern Masked Weavers ($p>0.6$).

Discussion

Averaged across all years, the duration of primary moult was shorter in Southern Masked Weavers than in the other two species (75 days vs 96 days). Primary moult started latest in Southern Masked Weavers, thus the duration is probably reduced to enable moult to end before mid winter. The duration of moult was 96 days in Cape Weavers (Table 1), starting on average on 12 November. Elliott (1973 p. 73) estimated the duration of moult to be 107 days from October to March; Craig *et al.* (2001) estimated moult duration to be 86 days, both in the Western Cape. Southern Red Bishop moult lasted 96 days, and started on average on 5 December. Craig *et al.* (2001) estimated moult to be 110 days, from November to April in the Western Cape. Southern Masked Weaver moult lasted 75 days, and started on average on 14 January. Oschadleus *et al.* (2000) estimated moult to be 74 days, starting on average on 9 January in the Western Cape.

There were differences of three to five weeks between the earliest and latest starting dates of moult for the three species. For Cape Weavers and Southern Red Bishops this wide variation in starting dates appeared to be due to variability in timing of rainfall at the end of the winter wet season in the study area. End of moult followed after breeding which was correlated with the end of the rainy season. The occurrence of rainfall is a key variable in triggering the onset of breeding in weavers in southern Africa (e.g. Martin and Martin 1970, Maclean 1973, Skinner 1995, Friedl 2002). The results here demonstrate that, in the winter rainfall region, the end of the wet season is a cue to terminate breeding and start primary moult.

The onset of moult between years in the Southern Masked Weaver was not related to the wetness index. For the first three years (1993–1995), the average data of commencement was mid-January; for the final six years (1998–2003), moult, on average commenced in the first week of January. The onset of moult therefore appeared to have advanced by about one week. It is possible that this relatively new arrival in the winter rainfall area of the Western Cape is slowly adjusting its breeding

seasonality to earlier in the spring, closer to the timing of breeding for most passerines in the region (see also Chapter 5).

Moult onset in different years probably depends more on the end of breeding season than the start or success thereof, because moult follows soon after breeding (Chapters 5–7). This is in accord with Elliott's (1973) study of breeding and moult in Cape Weavers in the Western Cape. He found that the last eggs were laid between 9 November and 25 November in four successive seasons (Elliott 1973, Table 4.3). Although he did not analyse moult rigorously, moult started within a two-week time span over four seasons (Elliott 1973, p. 64 and Table 5.7).

Southern Red Bishops in the Western Cape started moult two months after the first dry period in October. Friedl (2002) analysed breeding activity in relation to rainfall in a Southern Red Bishop population in the Addo National Park, Eastern Cape. Within breeding seasons he showed that peaks in egg-laying usually followed 10 to 20 days after large rainfall events. He found that breeding seasons lasted longer in years with good mid-seasonal rain (Friedl 2002). Thus, for Southern Red Bishops, both the start and termination of the breeding season seem to be influenced by rainfall. Breeding is often related to unseasonal rainfall, e.g. Rowan (1953).

From the present study, Southern Red Bishops seem to continue breeding for longer than Cape Weavers after the first dry period after October. A possible reason for this ability to breed for longer may be that Southern Red Bishop chicks are less dependent on insects than are Cape Weaver chicks; female Southern Red Bishops feed chicks both insects and seeds, while Cape Weavers feed mainly insects to their chicks (Fry and Keith 2004).

Both regression models relating the starting date of primary moult for Cape Weavers and Southern Red Bishops had slope coefficients which were less than one (0.73 and 0.82, respectively). This suggests that the period between the end of the wet period (considered here as a proxy for the end of the breeding season) and the onset of moult is shorter when the end of the breeding season is late than when it is early. As expected, it might be predicted that an extended breeding season would result in a short delay in the onset of moult. However, this result is based on relatively small sample size (n=10), and should be investigated further.

Annual variation in moult parameters has been studied in two non-passerines and seven passerines. In a six-year study, annual moult variation was related to male body mass in Cassin's Auklets (Emslie *et al.* 1990); timing of breeding and breeding

success varied annually but were not correlated with start of moult. Figuerola and Bertolero (1995) found variation in timing of moult in Curlew Sandpipers in a three-year study at a migration stop-over site; they suggested that start of moult was related to breeding success; females with a high breeding success probably delay start of wing-moult until they reach their wintering grounds. Start of moult was probably related to the end of breeding activity in any year in Dunnocks (Ginn 1975). A few Dunnocks caught in moult in different years showed no significant correlation between timing of moult in the same individual in different years. In a two-year study start of moult was related to the breeding effort in Pied Flycatchers, Siikamaki *et al.* (1994) suggested a trade-off between moult and current breeding; females with large clutches incurred an energetic cost and thus delayed start of moult. Sondell (2000) investigated timing and duration of moult in relation to weather in Reed Buntings in central Sweden for the period 1973–1995. The temperature in summer had a significant influence on the onset of moult and less effect on the duration of moult. Evans (1966) studied timing of breeding, moult and migration in Lesser Redpolls over three years and concluded that primary moult started when the last brood reached independence. Usually moult was completed by the time migration began. Morton and Morton (1990) studied moult in Mountain White-crowned Sparrows over eight years. Moult consistently started earlier and was longer in males than in females. Mean start of moult varied inter-annually by 17 days, and mean duration varied by 2.5 days in males and 4.0 days in females. Start of moult in Bullfinches varied annually in relation to end of breeding in a five-year study (Newton 1966, 1999). Start of moult varied by up to six days in three three-year periods in Cape White-eyes *Zosterops pallidus* in the Western Cape (Hulley 2004); he did not relate these inter-annual variations to any environmental factors.

Annual variations in primary moult parameters depend on the physiological state of the birds, and this could be measured in factors that affect the birds' energetic state like food availability, end of the breeding season, and breeding success. Dawson (2004) showed that Common Starlings *Sturnus vulgaris* that delay moult, do so with a measurable decrease in feather mass suggesting that late-breeding birds are likely to suffer a decrease in the quality of plumage grown during the subsequent moult.

Recording moult in birds is a time-consuming activity because large numbers of birds need to be sampled over many months. Studying inter-annual variation in moult is thus even more difficult, as is shown by the paucity of such studies. This

study covers the longest time period in comparing annual variation in moult parameters in three species in the same area.

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Table 1: Estimates of the primary moult parameters of adult Cape Weavers, Southern Red Bishops and Southern Masked Weavers in the Western Cape, 1993–2003

Species	Mean starting date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Standard error (days)	Mean completion date	Standard error (days)	n
Cape Weaver	12 Nov	1.1	23.1	0.5	95.9	1.6	16 Feb	1.0	3500
Southern Red Bishop	5 Dec	1.1	21.56	0.5	95.5	1.6	11 Mar	1.0	3742
Southern Masked Weaver	14 Jan	1.5	29.1	0.7	75.0	1.9	30 Mar	1.2	3226

Table 2: Estimates of the primary moult parameters of adult Cape Weavers, Southern Red Bishops and Southern Masked Weavers in the Western Cape, 1993–2003, for individual years

Year	Mean starting date	Standard error (days)	Mean completion date	Standard error (days)	n
Cape Weaver, duration 96.3 (1.7) days, s.d. 24.4 (0.5) days					
1993	27 Oct	4.7	31 Jan	6.7	496
1994	15 Nov	2.6	20 Feb	3.6	471
1995	14 Nov	2.9	18 Feb	4.0	427
1996	27 Nov	2.9	3 Mar	4.0	460
1997	15 Nov	4.7	20 Feb	6.4	311
1998	4 Nov	2.9	9 Feb	4.0	514
1999	1 Nov	2.4	5 Feb	3.2	526
2000	17 Nov	2.5	21 Feb	3.5	462
2001	9 Nov	2.4	14 Feb	3.4	552
2002	16 Nov	2.1	20 Feb	3.0	589
2003	13 Nov	2.2	18 Feb	3.2	554
Southern Red Bishop, duration 94.0 (1.5) days, s.d. 20.9 (0.5) days					
1993	2 Dec	3.2	7 Mar	4.6	97
1994	9 Dec	2.2	13 Mar	3.2	182
1995	12 Dec	3.2	16 Mar	4.7	87
1996	1 Jan	4.6	6 Apr	6.6	106
1997	11 Dec	5.3	15 Mar	7.6	126
1998	8 Dec	1.6	12 Mar	2.5	802
1999	27 Nov	1.6	1 Mar	2.5	449
2000	11 Dec	2.5	15 Mar	3.7	416
2001	13 Dec	1.8	17 Mar	2.8	560
2002	10 Dec	1.7	14 Mar	2.7	462
2003	6 Dec	1.9	10 Mar	2.9	455
Southern Masked Weaver, duration 74.7 (1.9) days, s.d. 29.2 (0.7) days					
1993	20 Jan	2.4	5 Apr	3.5	859
1994	18 Jan	1.9	3 Apr	3.0	691
1995	25 Jan	6.2	9 Apr	8.8	91
1996	9 Jan	6.2	25 Mar	8.8	87
1997	*Insufficient data*				
1998	6 Jan	4.6	22 Mar	6.6	255
1999	6 Jan	3.9	21 Mar	5.6	156
2000	9 Jan	4.5	25 Mar	6.5	170
2001	6 Jan	3.5	21 Mar	5.1	290
2002	8 Jan	2.9	24 Mar	4.3	333
2003	4 Jan	3.4	20 Mar	5.0	385

Figure 1: Capture sites for adult Cape Weavers, Southern Red Bishops and Southern Masked Weavers in grid 33°S 18°E in the Western Cape, South Africa, 1993–2003, showing sites from which primary moult data were obtained; Cape Weavers were captured on Dassen and Robben islands as well as on the mainland; the open circle indicates the Altydgedacht rainfall station

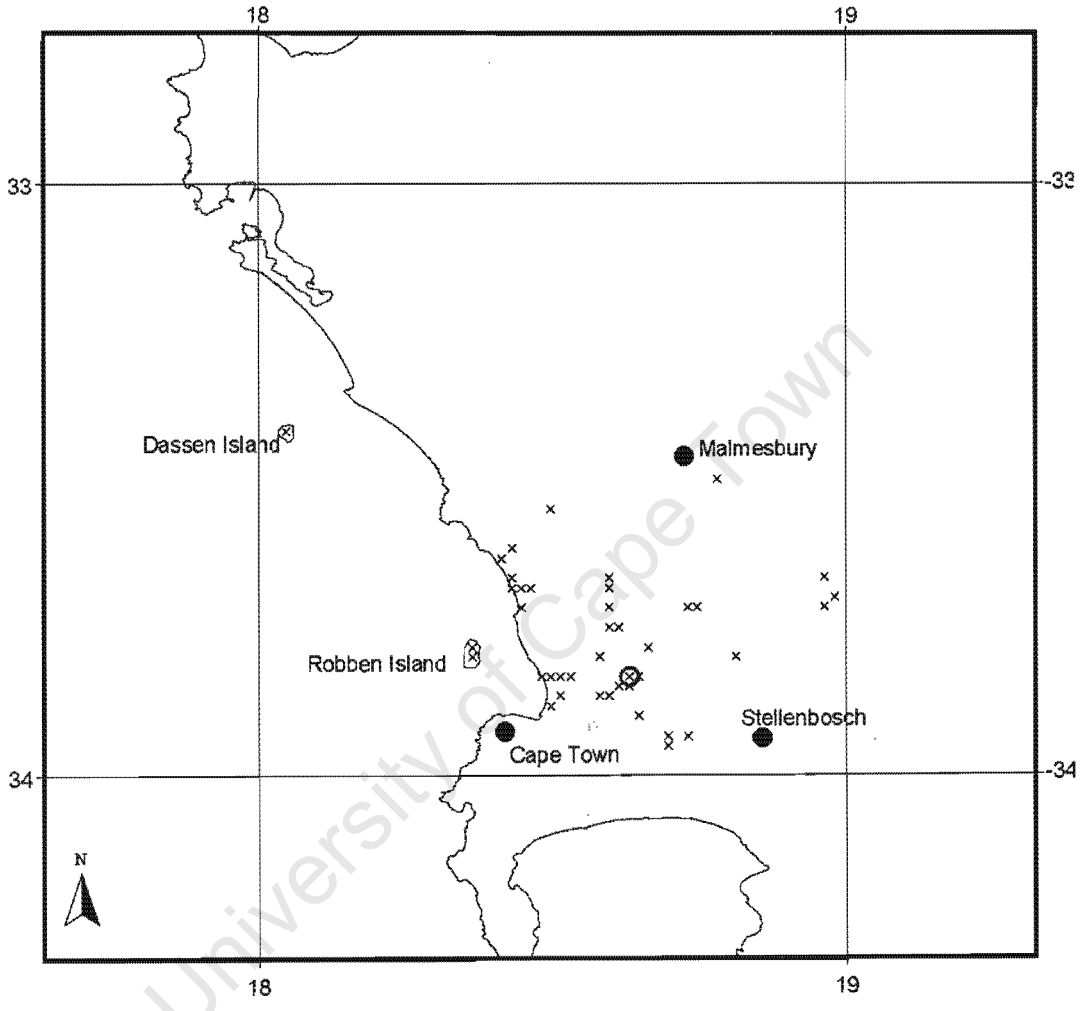


Figure 2: Estimated mean starting dates of primary moult for adult Cape Weavers (open squares), Southern Red Bishops (solid squares) and Southern Masked Weavers (solid triangles) in the Western Cape, South Africa, 1993–2003

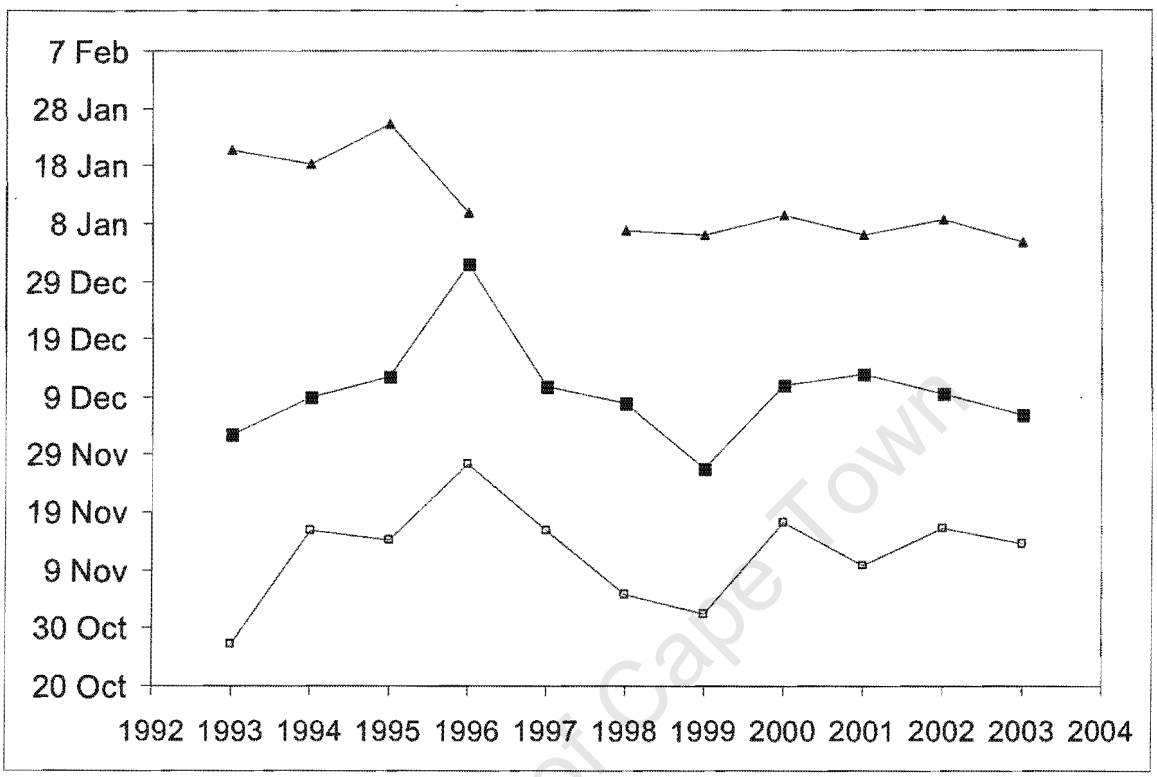


Figure 3: Relationship between the estimated starting date of primary moult in different years in Cape Weavers and Southern Red Bishops in the Western Cape, 1993–2003. The cluster of five points represents the years 1994, 1995, 1997, 2000 and 2002. The regression line is $y = 35.7 + 0.82x$, where x (days after 1 October) is the predicted day on which Cape Weavers commence moult and y (days after 1 October) is the predicted day on which Southern Red Bishops commence moult ($r^2 = 0.66$, P=0.001)

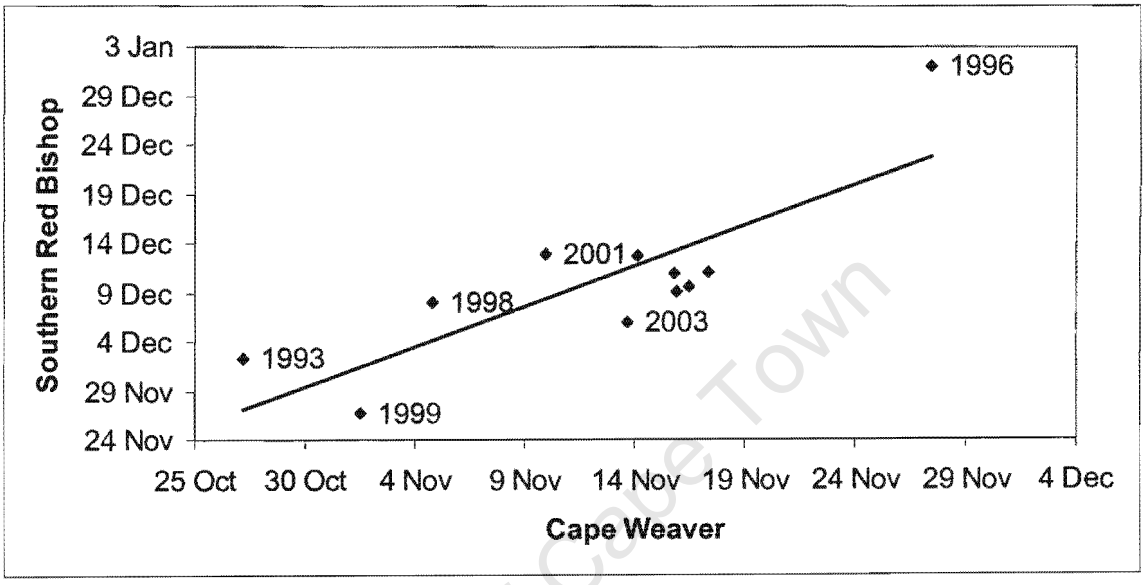
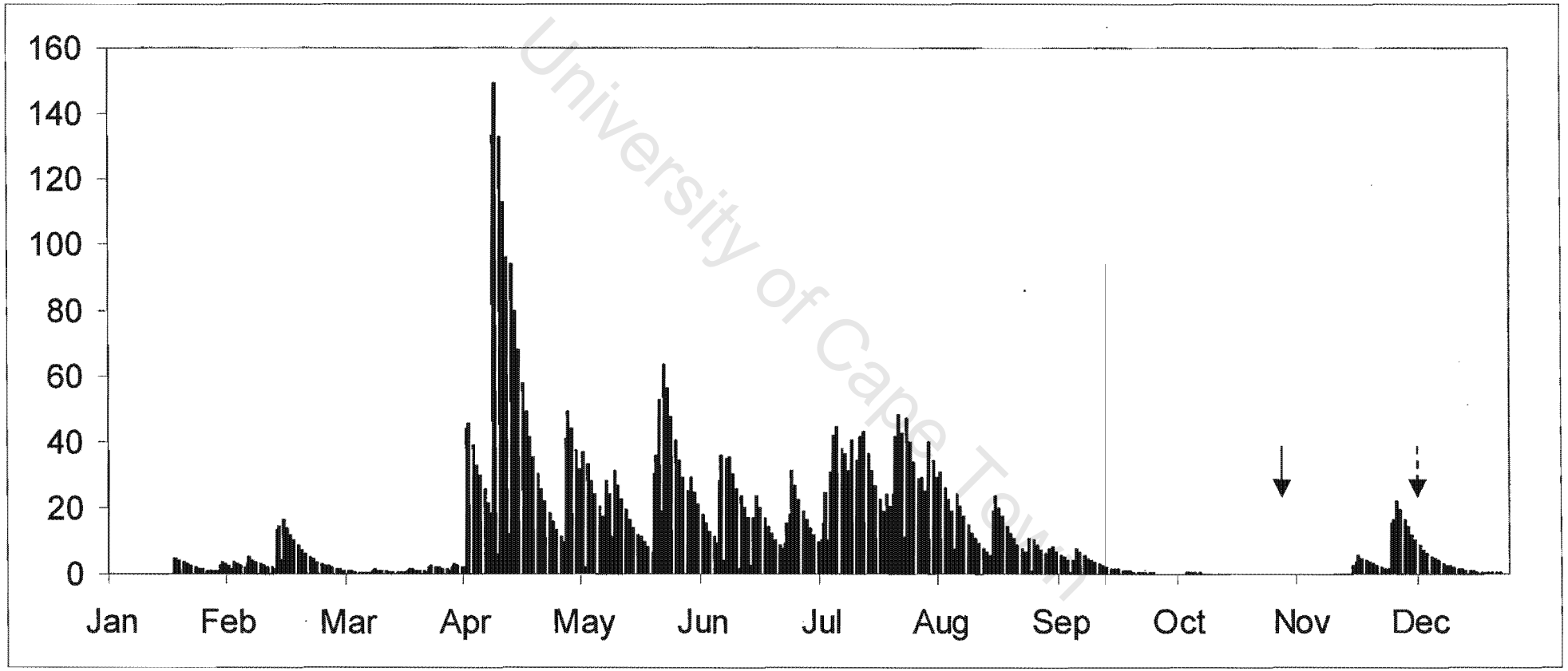
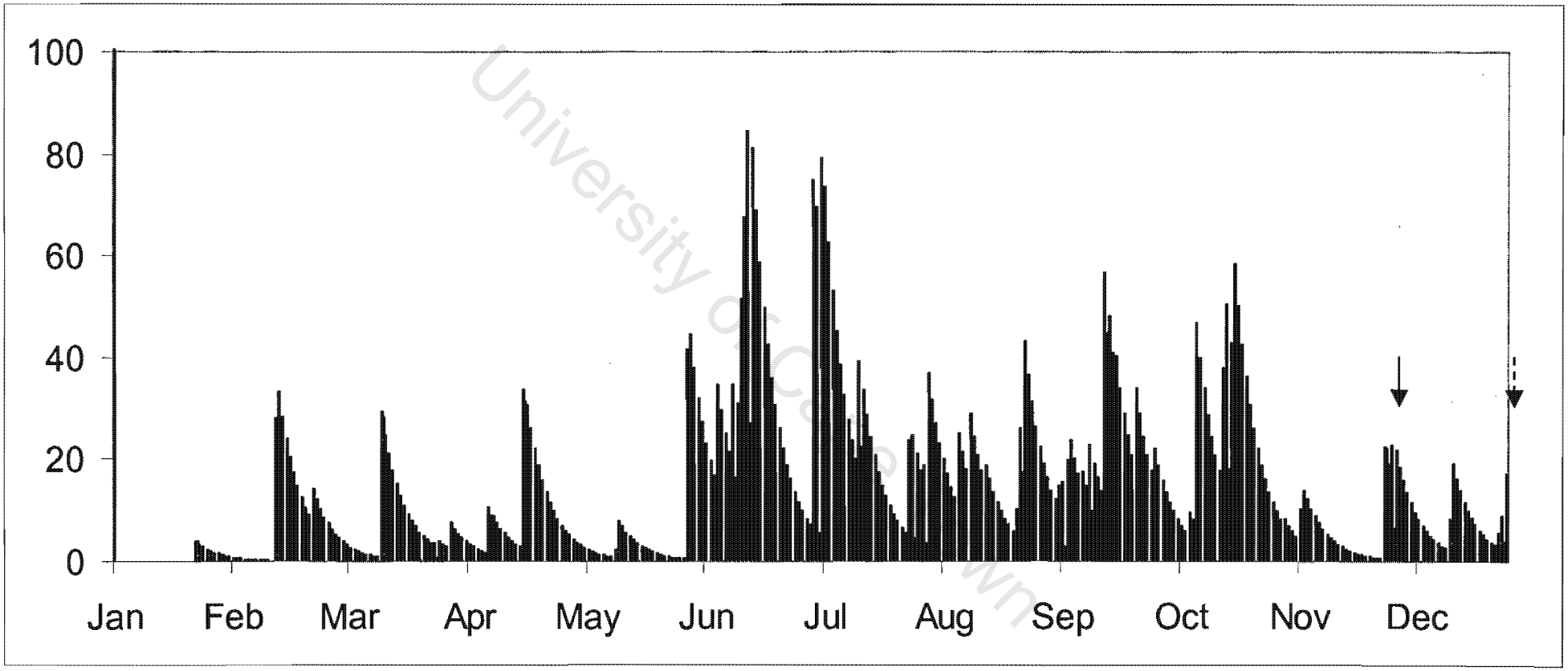


Figure 4: Daily wetness index (for description, see text) for selected years at Altydgedacht rainfall station in the Western Cape, South Africa

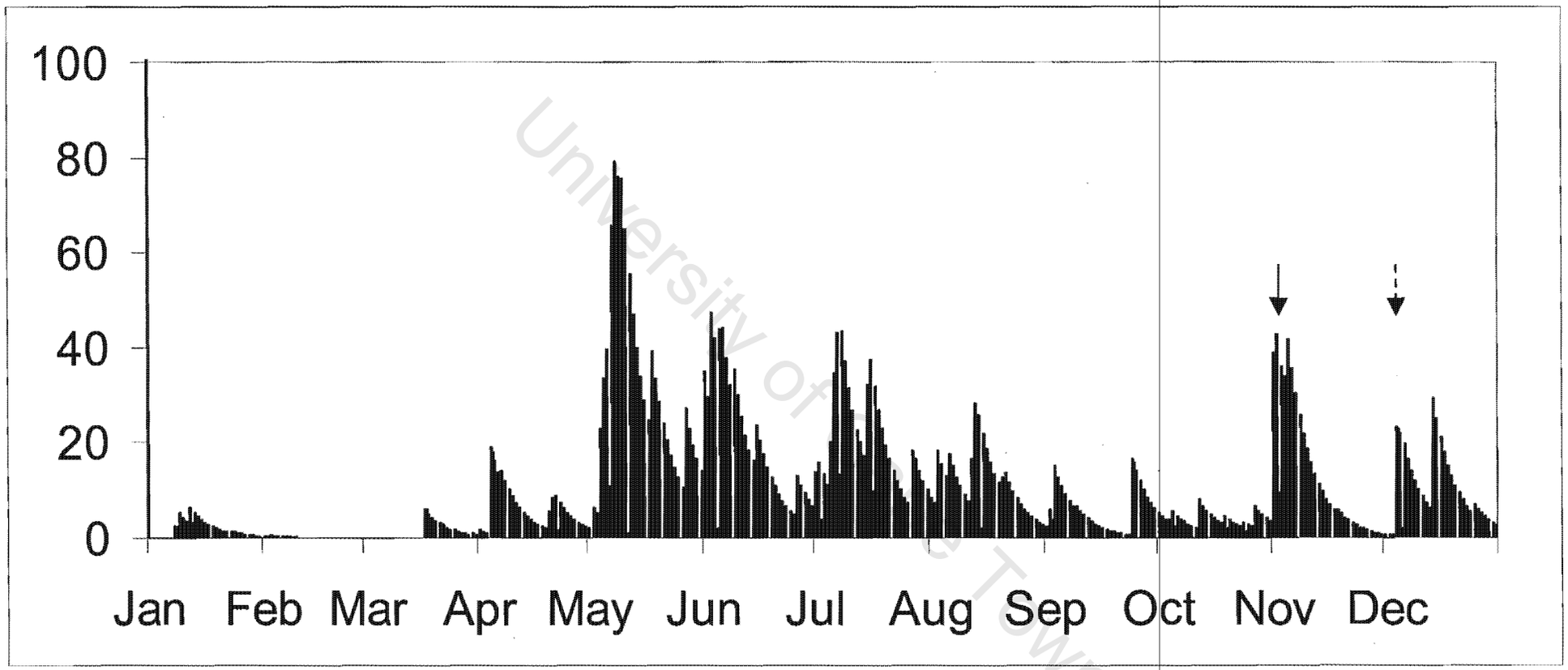
(a) 1993, an early wet winter but dry October. Mean date of start of primary moult for Cape Weavers was 27 October (solid arrow), 26 days after 1 October, and for Southern Red Bishops (broken arrow) was 2 December, 62 days after 1 October



(b) 1996, a wet winter and wet spring. Mean date of start of primary moult for Cape Weavers (solid arrow) was 27 November, 57 days after 1 October, and for Southern Red Bishops (broken arrow) was 1 January, 92 days after 1 October



(c) 1998, a wet winter, relatively low spring rainfall, new rains in November. Mean date of start of primary moult for Cape Weavers (solid arrow) was 4 November, 34 days after 1 October, and for Southern Red Bishops (broken arrow) was 8 December, 68 days after 1 October



Chapter 9

Annual cycles in southern African weavers: breeding seasonality and moult patterns

Annual cycles in southern African weavers: breeding seasonality and moult patterns

Introduction

With 116 species, the weavers comprise a large family with a wide diversity of life histories, as highlighted by Crook (1964). Lack (1968) acknowledged that Crook's approach to the study of ecological adaptations in weavers formed part of the inspiration for his classic text *Ecological adaptations for breeding in birds*. Of all passerine families, the weavers, along with the blackbirds Icteridae of North and South America, show the greatest diversity in breeding habits (Lack 1968). This diversity is also seen in the diversity of timing and duration of primary moult presented in this thesis. Moult has been studied in several southern African species previously, but only two papers (Oschadleus *et al.* 2000, Craig *et al.* 2001) used a rigorous statistical technique (the Underhill-Zucchini model) that allows precise comparisons between species and geographic areas.

This chapter is an overview of the preceding chapters and summarizes the annual cycle of southern African weavers, in particular the timing of breeding and post-nuptial moult. First, however, the relative wing shapes of southern African weavers are discussed.

Relative feather masses

Weaver wing shapes are fairly uniform in that the primaries increase in size from the innermost and then decrease near the outermost primaries. There is variation on a finer scale as to which primary is the largest, and in the extent of reduction of the 10th primary. In the Ploceidae generally the degree to which the outermost (10th) primary is reduced is subject to much variation. Moreau (1960: 449–451) studied the length of the outer primary in a large number of weavers and found no correlation with taxonomy or habitat.

The primary feathers of the wings were weighed, in order to calculate relative feather masses, for Sociable Weavers *Philetairus socius*, Chestnut Weavers *Ploceus rubiginosus*, Thick-billed Weavers *Amblyospiza albifrons*, Lesser Masked Weavers

Ploceus intermedius, White-winged Widows *Euplectes albonotatus* and Long-tailed Widows *E. progne* (Table 1). In addition, relative feather masses were obtained from the literature for Cape Weavers *Ploceus capensis* (Underhill and Joubert 1995), Southern Masked Weavers *P. velatus* (Oschadleus *et al.* 2000), Village Weavers *P. cucullatus*, Red-billed Queleas *Quelea quelea* and Southern Red Bishops *E. orix* (Craig *et al.* 2001). Primary moult parameters for Lesser Masked Weavers were not included in this thesis because the available sample size was small.

Plotting the individual primary feather mass percentages showed an increase in percentage mass from Primary 1 to Primary 9, although the relative masses of Primaries 8 and 9 are similar (Figure 1). Primary 10 is small in all species, accounting for between 0 and 2% of total primary feather mass (Table 1). All weaver wings analysed showed a rounded wing, across different genera. Thick-billed Weavers, Long-tailed Widows, and to a lesser extent Sociable Weavers, however, had more rounded wings than those of other weavers, with the feather mass of Primary 9 being less than Primary 8 (Figure 1). These three species differ in size and are in different genera.

Within the four *Ploceus* species there was little variation in relative feather masses (Table 1); most of the variation related to the extent of reduction in Primary 10. Craig *et al.* (2001) did not provide masses for Primary 10 in Village Weavers; in this species Primary 10 is vestigial (pers. obs.).

Potential factors influencing wing shape are protection against physical abrasion and aerodynamics (take-off, migration, flight displays). Thus Sociable Weavers may have rounded wings to protect the outer primaries from abrasion on their nests (see Chapter 2). Dawson (2005) suggested that, in a range of European passerines, that the greater relative mass of the outer primaries in some species may reflect a protective role against physical abrasion, or an aerodynamic role in that each of these feathers provides a leading edge to the wing. He found that scaling relationships (log mass vs log length) were related to flight characteristics and habitat, rather than to phylogeny.

In European Starling *Sturnus vulgaris*, take-off parameters vary with wingtip shape; birds with more rounded wingtips tended to take off from the ground at a steeper angle of ascent than those with relatively more pointed wingtips (Swaddle and Lockwood 2003). Given the wide variety of flight activities of the weaverbirds, an inter-species

analysis of wingtip shape with the ploceids is likely to be a rewarding avenue for future research.

Wing shape is related to migration, with long-distance migrants having more pointed wings (Underhill and Joubert 1995). Weavers are not long distance migrants, and the longest movements occur in Red-billed Quelea (Jones 1989). Chestnut Weavers are resident in some areas but show regular movements in others, often correlated with rainfall (Fry and Keith 2004); the longest known movement is 213 km in East Africa (Backhurst 1977) and 284 km in southern Africa (Oschadleus and Brooks 2005). These two species, Chestnut Weaver (males) and Red-billed Quelea, have the most pointed wings of the weaver species for which data are available, with the relative mass of Primary 9 being greater than 14.5% (Table 1).

Long-tailed Widows have larger wings in males than in females to compensate for the aerodynamic costs of a large tail in the male (Balmford *et al.* 1994). This may also be a reason for the more rounded shape of the wing in this species compared to other species. The difference in relative primary feather masses between males and females is worth investigation. The only species in which only the male has a long tail and for which feather mass data for both sexes are available is the Cape Sugarbird *Promerops cafer* (Underhill and Joubert 1995); their data shows considerable differences between the sexes. Male sugarbirds use their wings to produce a snapping sound in display flights, and this may explain part of the difference in relative primary masses between males and females in this species (Skead 1967).

Underhill and Joubert (1995) modelled wing shapes using relative masses of primary feathers, using second order Tchebycheff polynomials in a regression analysis, to describe the shape of a bird's wing with two parameters. The same method was employed here using the first nine primaries of the weavers. The advantage of using Tchebycheff polynomials is that the estimates of the regression coefficients are uncorrelated with each other (Underhill and Joubert 1995). This method produces three regression coefficients, denoted R, S and T. Underhill and Joubert (1995) showed that the coefficient R is of no interest in describing wing shape, and that S and T summarize the manner in which relative primary masses change. A plot of S vs T thus summarizes the nine-dimensional relative feather mass data in a two-dimensional plot; Underhill and Joubert (1995) plotted

S vs –T, and this convention is followed here. If a species has both S=0 and T=0, all nine primaries are of equal mass; if both S and T of a species are near to zero, so that are close to the origin in the plot, the species must have a relatively uniform set of primaries.

Figure 2 provides a plot of S vs –T for the 11 species of weavers for which data are available. The Red-billed Quelea has a relatively large positive value for S and T is nearly zero; Underhill and Joubert (1995) show that this indicates that the feather masses form a geometric progression from the smallest (innermost) to the largest (outermost) primaries. Both male and female Chestnut Weavers have large positive values for S and small negative values for T (Figure 2). This indicates that the rate of increase in mass decreases for the outermost primaries; however in this species the outermost primary is still the heaviest. The Thick-billed Weaver and Long-tailed Widow have a relatively small positive values for S and large negative values for T; this is characteristic of species for which the outermost primaries are not the largest. Most of the remaining weavers in Figure 2 have intermediate values for both S and T, indicating that that the rate of increase in mass decreases for the outermost primaries, but several of the outermost feathers may be similar in mass. The potential of the approach to describe one aspect of wing shape pioneered by Underhill and Joubert (1995) should be further explored with a larger sample of species.

Breeding in southern Africa weavers

In the eastern parts of southern Africa, especially KwaZulu-Natal, peak summer rainfall is in December; farther north in Zimbabwe, the peak is in January; to the west, in Botswana and Namibia, peak rainfall occurs in late summer, in January and February (Allan *et al.* 1997; see Figure 1 of Chapter 1). The overall pattern is that the time of peak rainfall across the summer rainfall region of southern Africa moves in an anticlockwise direction. Most granivorous birds in the summer rainfall region breed in mid- to late summer, in response to rain which results in a flush in insect abundance to feed their young and also results in seed crops from rains several weeks earlier (Skinner 1995).

The peak breeding was plotted as a median for each species per region, using the data from the BirdLife South Africa Nest Record Card Scheme (NRC) (RP Prŷs-Jones

and I Newton unpublished data). Peak breeding in the Western Cape was in September for the four weaver species that occur there (Appendix 1). Peak breeding for all other regions was more spread out for different species, and occurred mainly in summer with some records in late spring or autumn (Figure 3).

Breeding in the winter rainfall region is towards the end of the wet season, and in the summer rainfall regions at the start of the wet season. In the winter rainfall region breeding does not take place at the start of the wet season, because temperatures are then low and falling, so that vegetation and insects are slow to respond to the rain (Moreau 1950). Breeding is postponed until late in the wet season, when temperatures are increasing (Figure 4a). In contrast, in the summer rainfall region temperatures are rising when the rainy season begins so vegetation and insects appear soon after the rain starts (Moreau 1950), allowing breeding to commence soon after the rains begin (Figure 4b). In arid regions breeding seasonality depends on rainfall which is variable, both in timing and quantity (Tyson 1987). Southern Masked Weavers have been recorded breeding along the Kuiseb River when the river flooded even though the rainfall which had generated the flood, and consequent insect flush, was in a distant catchment area (Jensen 1972). Sociable Weavers lay eggs after rainfall with a lag of as little as six days (Maclean 1987). In arid regions, birds breed when there is no rain, e.g. Chestnut Weavers (Komen and Buys 1990), but clutch size is reduced relative to years with higher rainfall (Lepage and Lloyd 2004). Average clutch sizes in Southern Red Bishops were related to the amount of rainfall during the breeding season, with a larger average clutch size in seasons with a higher amount of rainfall (Friedl 2002). Thus rainfall, rather than evapotranspiration, has been regarded as the most important determinant of primary productivity in the arid regions of South Africa (Lepage and Lloyd 2004).

Several studies show that the timing of the breeding season in the Southern Red Bishop is usually related to rainfall. Craig (1982) found that Southern Red Bishop clutches were mostly laid in, or shortly after, the rainy season throughout the summer rainfall region of southern Africa. Craig (1982) also found that a high amount of rainfall preceding the breeding season corresponded to high breeding activity within that season. Friedl (2002) analysed breeding activity in relation to rainfall in a Southern Red Bishop population in the Addo National Park, Eastern Cape. He found that in seasons with poor

rainfall, breeding activity as measured in terms of the total number of nests built and total number of eggs laid during a breeding season was reduced. A detailed study on the temporal pattern of rainfall and breeding activity within breeding seasons showed that peaks in egg-laying usually followed 10 to 20 days after major rainfall events; the total number of eggs laid corresponded to the amount of rainfall in the preceding rainfall peak and showed that poor rainfall preceding breeding delayed the start of the breeding season. This was also recorded by Brooke (1966a) studying Southern Red Bishops in Zimbabwe.

The breeding season of Southern Red Bishops in the Eastern Cape was often characterised by two distinctive breeding peaks with a period in between in which there were only few or even no nests at all that contain nestlings or incubated eggs (Friedl 2002). Between the breeding peaks the general activity level was reduced and the males spent considerably less time on the territory, until good rains initiated the second breeding peak and the males started with nest-building again (Friedl 2002). In contrast to the Eastern Cape, rainfall does not seem to affect the temporal pattern of breeding activity within a season in KwaZulu-Natal (Craig 1982).

The termination of the breeding season is also influenced by rainfall, with breeding seasons of Southern Red Bishops lasting longer in years with good mid-seasonal rain (Friedl 2002). The first indication of the end of the breeding season is the termination of nest-building by the males. Gradually other activities such as territorial displays and courtship behaviour decrease in frequency and the males spend less time on their territories. Soon after they have started the postnuptial moult the first males leave the colony. Some of the territorial males will stay longer, and these are usually males with nests that contain incubated eggs or chicks (Friedl 2004).

Breeding by weavers in the summer rainfall region of southern Africa is usually in summer, but it is often delayed or advanced by unseasonal rainfall (Table 2). Southern Masked Weavers bred early in Namibia after heavy rains (Immelmann and Immelmann 1968). Southern Masked Weavers and White-winged Widows showed breeding behaviour after late rains over wide areas in the northern and central parts of the Kruger National Park (Johnson 1983). Other records of early or late breeding in response to late rains (Table 2) are from the Karoo, Northern Cape, Botswana and Namibia, i.e. semi-arid

regions, where seasonality of rainfall is more variable than in the more mesic eastern parts of southern Africa. Even with the winter rainfall region in the Western Cape, rainfall events cause perturbations in the timing of breeding: Cape Weavers started breeding in June, when temperatures in the region are generally decreasing, after a very wet April (Rowan 1953).

In this thesis, the breeding season was defined as the period of egg-laying. Breeding cycles, i.e. mean incubation plus mean fledging periods, in southern African weavers, last three to five weeks: 22–38 days (Table 3). Breeding cycles are related largely to bird size (Table 3), so larger weavers have a longer breeding cycle. The shortest breeding cycle is that of the Red-billed Quelea, at 21.5 days. Lloyd (2004) found that the incubation periods of some *Eremopterix* sparrow-larks and Red-billed Quelea are at least two days shorter than those reported for any other African species. The shared features of their ecology that might select for very short incubation periods are their high degree of nomadism and typically short windows of opportunity for breeding. The length of a breeding cycle is a key component in determining where moult should be located within this annual cycle (see also Figure 4). In the case of breeding after unseasonal rainfall, there needs to be enough rainfall to sustain a breeding cycle.

Patterns of moult in southern Africa weavers

The major outcome of this thesis has been the application of the moult model of Underhill and Zucchini (1988) to 15 species of ploceids in southern Africa (Table 4). For seven of these species moult parameters are now available for more than one locality, and for the Southern Masked Weaver independent estimates are available for two time periods, so that there are a total of 31 sets of primary moult parameters (Table 4). This excludes the 32 sets of annual estimates of moult parameters in Chapter 8. This approximately doubles the number of available sets of estimates of primary moult parameters (see Table 2 of Chapter 1).

The duration of primary moult in some arid-region weavers, namely White-browed Sparrow-weavers *Plocepasser mahali* and Scaly-feathered Finches *Sporopipes*

squamifrons, the Underhill-Zucchini model is not usable because the moult patterns are irregular (pers. obs.).

There is remarkably little available information relating to the primary moult of weavers from elsewhere in Africa (Chapter 1, Table 2). With two exceptions, papers which allude to primary moult of weavers unfortunately present only the moult scores for a very small sample of captured birds or contain a vague comment about the timing and/or duration of moult.

Two studies deserve further mention. Hanmer (1984) studied Southern Brown-throated Weaver *Ploceus xanthopterus* in Mopeia, Mozambique, and Nchalo, Malawi. The breeding season in Nchalo is from October to April, but actual dates in any year were dependent on rainfall. Males started moult while there were eggs or chicks in the nests, whereas females started moult immediately after the last brood left the nest. Duration of moult was estimated from the change in moult scores of recaptured birds, giving 87 days for adult males and 98 days for adult females.

Brooke (1985) studied the annual cycle in Seychelles Fody *Foudia sechellarum* on Cousin Island. This species is the only weaver known to have a regular pre-nuptial primary moult. Primary moult is concentrated in the months February to May, followed by breeding in the months May to September. Duration of moult was estimated from the change in moult scores of recaptured birds and averaged 101 days in 1978 and 89 days in 1979. The annual cycle consists of moult, which Brooke (1985) estimated to last three months, followed by nesting (minimum 1.5 months), caring for fledged young (up to four months), and a possible lean period (2–3 months).

Within the southern African database (Table 4), the results in this thesis indicate that moult followed soon after breeding in all species other than Sociable Weavers. By species and area, primary moult started between 11 November and 31 May, a range of nearly six months; the earliest dates were all in the Western Cape (Table 4, Appendix 2). The completion date of moult varied between 17 February and 5 November, an even longer range of 10.5 months; moult ended first in the winter rainfall region, then in the mesic part of the summer rainfall region along the east coast, and lastly in the arid regions in the western interior.

The duration of primary moult in southern African weavers also varied widely in different species and different areas, from 1.6–7.2 months (Table 4). Duration was longer at 5.1–6.9 months in the two species restricted to arid and semi-arid regions of northern Namibia, namely Sociable and Chestnut Weavers. Duration is shorter in the eastern summer rainfall region of southern Africa (in particular *Euplectes* species), ranging from 1.6–4.1 months (median 2.8 months). The Red-billed Quelea is found in both the arid west and in the wetter east. Its duration, however, is longer in the mesic east (3.4–4.1 months) than in the dry west (2.5–2.8 months).

In sexually dimorphic species, there seems to be a tendency for male weavers to start moult earlier then females, e.g. Chestnut Weavers (Chapter 3). Elliott (1973) found male Cape Weavers to moult three weeks earlier than females. Hanmer (1984) found that in Southern Brown-throated Weaver, the males started moult while there were eggs or chicks in the nests and females started moult after the last brood left the nest. The sexual difference in onset of moult is partly because the males are polygynous and leave the colonies while the females finish breeding. Craig and Manson (1979), however, found no sexual difference in onset of moult in the polygynous Southern Red Bishops, Red-collared Widows *E. ardens* and Fan-tailed Widows *E. axillaris*. Laycock (1982) found little or no difference between males and females in onset of moult in Thick-billed Weavers. There are not likely to be differences between sexes in start date of moult in monogamous species, such as Spectacled Weaver *P. ocularis*.

The length of the breeding cycle places an upper limit on how far in advance of females the males could start moult. In this thesis, sexual differences in start of moult were noted in Chestnut Weavers, but were not investigated in other species due to lack of adequately sized samples of reliably sexed birds. This is because many weaver species are difficult to age and sex, especially in their non-breeding plumage. There is a need to develop ageing and sexing criteria for weavers, and for the production of a guide analogous to that of Svensson (1992), which in its successive editions has steadily refined the ageing and sexing criteria for passerines in Europe, and is extensively used by ringers.

In the monogamous weavers, both males and females can be expected to start moult at the same time because they share incubation and nesting duties equally. There were enough data to estimate the parameters of moult for only one monogamous *Ploceus*

weaver in this study, the Spectacled Weaver. Monogamous *Ploceus* weavers are solitary and often found in forest habitats, making it a challenge to obtain samples sizes sufficient to undertake analyses of primary moult, e.g. Dark-backed Weaver *P. bicolor*, of which 112 birds have been ringed in southern Africa in the period 1948–2001 (Oschadleus 2002).

Two species, the Southern Masked Weaver (see Chapter 8) and Thick-billed Weaver (see Chapter 7), have undergone range expansions in the last century and the new populations appear to show evolving patterns in the timing of moult. Both species have advanced the timing of breeding and onset of moult relative to the areas from which they presumably originated, clearly an adaptation to local environmental conditions. Several species of ploceids continue to undergo range expansions, and this will provide further opportunities to study adaptations to timing of breeding and primary moult in relation to a new environment. In particular, the species that is likely to present a major opportunity in this direction is the Red-billed Quelea; this species is being mist-netted by ringers in the Western Cape with increasing frequency (Tygerberg Ringing Unit 2003, SAFRING unpubl. data). Given the rate of range expansion and establishment into the KwaZulu-Natal Midlands, and the Eastern Cape, the colonization of the winter rainfall region appears to be inevitable. Although this will be an event of alarming proportions to the extensive cereal-farming regions of the Swartland and Overberg, it will present an opportunity to investigate pace and progress of the patterns of change in the annual cycle of a species confined to the summer rainfall region when confronted with a winter rainfall regime. The opportunity to study these adaptations when the Southern Masked Weaver invaded the Western Cape between the 1940s and 1970s was lost.

Individual primary feather growth rates

The number of primaries growing simultaneously varied between an average of 1.0 and 2.3 feathers (Table 5, Figure 5). Craig and Manson (1979) obtained slightly higher values for individual number of feathers growing in *Euplectes* species in KwaZulu-Natal than in the present study: Southern Red Bishop 1.98, Red-collared Widow 2.57, Fan-tailed Widow males 2.30 and Fan-tailed Widow females 2.63. Laycock (1982) recorded an

average of 1.75 primaries growing simultaneously in Thick-billed Weavers in KwaZulu-Natal. Brooke (1985) measured an average of 2.4 primaries growing simultaneously in Seychelles Fodies. Figure 4 shows the rate of growth of the individual primaries for several weaver species.

The number of growing primaries seems to be related broadly to environment, and not to the overall speed of primary moult. In the species in arid regions 1.0–1.2 feathers grow simultaneously on average. In the eastern parts of southern Africa 1.6–2.3 feathers grow simultaneously. These numbers are biased in that when a bird starts and ends moult less primaries will be growing than during moult of the middle primaries. In the arid areas, the moult of the quelea is much shorter than that of the Chestnut or Sociable Weavers, yet all of them are moulting about one feather at a time. (The growth of one feather of the quelea is more rapid than that of a Chestnut or Sociable Weaver.) A possible reason for growing one primary at a time in arid regions is that it allows birds to suspend moult more easily than if several primaries are growing simultaneously, and to commence breeding if a rainfall event occurs. In mesic regions, birds can moult several primaries simultaneously as food is less likely to be a limiting factor. Thus weavers in mesic areas moult approximately two feathers simultaneously, but the rate of growth of individual primaries can vary to determine the overall length of moult which needs to be fitted into the annual cycle.

Conclusion

The annual cycle of birds is affected by the environment in which they live. Southern Africa is a large region, with a wide variety of climatic factors. This has an effect on bird distributions within the region (e.g. Harrison *et al.* 1997), as well as an effect on life-history parameters (Lepage and Lloyd 2004).

The weavers in the drier parts breed in summer but due to the variability in rainfall, often breed in response to rainfall at any time of year. Primary moult is protracted in species found mainly in arid regions. The weavers in the mesic east have well defined breeding periods, followed by primary moult. No weavers are restricted to the winter rainfall region; the four species that occur breed and moult earlier than

weavers elsewhere in southern Africa. The two weavers that show the most movement within southern Africa, the Red-billed Quelea and Chestnut Weaver, have the most pointed wings of the weavers studied. These two species show some temporal coordination of moult, particularly in the termination of moult being synchronized within each species.

This thesis provides the most comprehensive primary moult data available on an African group of birds, high-lighting general trends across species and climatic regions, as well as illustrating individual species adaptations. Rainfall patterns affect breeding seasonality and timing of moult while aridity affects number of primaries growing simultaneously. Enormous potential resides in the SAFRING database to study moult in southern Africa.

Finally I list a set of key findings:

- Sociable Weaver show variation in average body mass and wing length which is not clearly correlated with region, season or climate, other than a negative correlation of body mass with average annual water deficiency (Chapter 2).

- Body mass of Sociable Weavers near Kimberley showed a long-term decrease of 2.9 g, probably related to the prediction that body mass probably results from a trade-off between the risks of starvation at low mass and predation at high mass (Chapter 2).

- Individual primaries of Sociable Weavers were moulted mainly one at a time, each taking 20–28 days to grow fully. Prolonged duration of moult in this species is probably an adaptation to reduce energy expenditure, and to grow more durable feathers due to abrasion when entering the nest (Chapter 2).

- The lack of clear patterns of geographical variation in biometrics suggests that the contiguous populations of Sociable Weaver should belong to the nominate subspecies (Chapter 2).

- For both male and female Chestnut Weavers from northern Namibia wing length declined during and after the breeding season due to extensive feather wear (Chapter 3).

- Adult male Chestnut Weavers started primary moult three weeks earlier than females and moult lasted 17 days (9%) longer (Chapter 3).

- The onset and duration of primary moult in Red-billed Quelea in southern Africa varied substantially by region but completion of primary moult was well synchronized, ending in August in all sub-regions (Chapter 4).

- Rate of production of feather mass in Red-billed Quelea was remarkably uniform in different regions; moult speed was adjusted by the number of primaries growing concurrently – fewer feathers grew simultaneously when moult was faster. Counter-intuitively, a shorter duration of moult (i.e. fast moult) was achieved by growing fewer feathers concurrently but growing them faster (Chapter 4).

- The peak breeding seasons of Cape and Southern Masked Weavers coincided throughout South Africa, in all areas studied, except in the Western Cape where breeding by Southern Masked Weavers was delayed by a month relative to that of Cape Weavers. In these two weavers, and in the Red Bishop, primary moult started in the month within which the last eggs were laid (Chapter 5).

- The Southern Masked Weaver expanded its range into the south-western part of the Western Cape, and here it has advanced its peak breeding and moult onset by one month relative to other areas, but is still one month behind that of the Cape Weaver (Chapter 5).

- The number of primaries growing simultaneously in four species of widow-birds in South Africa was similar in these species (Chapter 6).

- The breeding seasonality of several *Ploceus* species is similar in the Eastern Cape and former Transvaal regions, both also being summer rainfall areas, but there was greater variability than in KwaZulu-Natal (Chapter 7).

- The Thick-billed Weaver had a similar durations of primary moult in Gauteng and KwaZulu-Natal of 71 and 73 days respectively, but the start date was five weeks earlier in Gauteng, an area to which the species has expanded in recent decades, for reasons which are not clear (Chapter 7).

- Annual variation in the starting dates of primary moult in Cape Weavers and Southern Red Bishops over 11 years in the Western Cape was correlated to variability in timing of the end of the wet winter season in different years; no similar pattern was detected for Southern Masked Weavers (Chapter 8).

- The onset of primary moult in the Southern Masked Weaver in the Western Cape shifted earlier; the species expanded its range into this new environmental in the middle of the 20th century, and it is proposed that the species is still adjusting the timing of its breeding and moult cycles (Chapters 5, 8).

- The weavers in the drier parts breed in summer but due to the variability in rainfall, often breed in response to rainfall at any time of year. Primary moult is protracted in species found mainly in arid regions. The weavers in the mesic east have well defined breeding periods, followed by primary moult. No weavers are restricted only to the winter rainfall region; the four species that occur breed and moult earlier than weavers elsewhere in southern Africa (Chapter 9).

- The annual cycle of southern African weavers was less variable in the mesic eastern part of southern Africa than in the arid west. The more regular rainfall of

the mesic regions allowed weavers to grow more than one primary simultaneously (1.6–2.3 feathers). In the arid regions weavers grew one primary at a time (1.0–1.2). Thus the number of growing primaries seems to be related broadly to environment, and not to the overall speed of primary moult (Chapter 9).

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Table 1: Mean relative masses of each primary feather of selected species of weavers in southern Africa (see text and Underhill and Joubert 1995 for further detail); the heaviest feather for each species is underlined

Primary	1	2	3	4	5	6	7	8	9	10	Source
Sociable Weaver	8.5	9.1	10.0	10.9	11.6	12.6	12.4	12.7	12.2	0.0	Chapter 2
Chestnut Weaver female	8.0	8.4	8.8	9.8	11.4	12.4	12.9	13.4	13.6	1.3	Chapter 3
Chestnut Weaver male	7.7	8.1	8.6	9.5	10.8	12.4	13.1	14.1	14.5	1.4	Chapter 3
Thick-billed Weaver	9.5	10.2	10.3	10.9	11.9	12.3	11.8	11.0	10.1	1.9	Chapter 7
Village Weaver	8.6	9.0	9.6	10.3	11.5	12.5	12.6	13.1	12.8	0.0	Craig *et al.* 2001
Cape Weaver	8.4	8.9	9.7	10.3	11.4	12.3	12.5	12.8	12.4	1.3	Underhill and Joubert 1995
Southern Masked Weaver	8.7	9.0	9.5	10.5	11.6	12.1	12.3	12.3	12.1	2.0	Oschadleus *et al.* 2000
Lesser Masked Weaver	8.9	9.7	9.6	10.6	11.5	11.7	12.0	12.1	12.6	1.4	Chapter 9
Red-billed Quelea	8.0	8.9	9.1	9.9	11.3	12.1	12.3	13.6	14.9	0.0	Craig *et al.* 2001
Red Bishop	8.3	8.8	9.4	9.9	11.7	12.4	12.6	12.9	14.0	0.0	Craig *et al.* 2001
White-winged Widow	9.3	9.6	9.8	10.4	11.6	11.8	12.0	12.5	13.0	0.0	Chapter 6
Long-tailed Widow	9.3	9.8	10.5	11.5	12.2	12.7	12.3	11.4	9.9	0.4	Chapter 6

Table 2: Unseasonal breeding in southern African weavers; published records of weavers breeding earlier or later than usual due to early or late rainfall events in southern Africa. Locality abbreviations for South African provinces and regions: N Cape = Northern Cape, KNP = Kruger National Park, W Cape = Western Cape

Area	Early or late rain	Rainfall	Breeding notes	Reference
Scaly-feathered Finch				
N Cape	late	heavy rain in April	nest building next day	Winterbottom (1967)
N Cape		first good rain shower	eggs laid 8 and 35–46 days after rain	Maclean (1971)
Sociable Weaver				
N Cape	none	drought	many colonies abandoned	Brooke (1987)
Southern Masked Weaver				
Namibia	early	heavy rain on 29 September	eggs & chicks 17–23 Oct 1965	Immelmann and Immelmann (1968)
Karoo	late	heavy rain Jan–Mar	eggs in March	Martin *et al.* (1986)
N Cape		first good rain shower	eggs laid 14 and15 days after rain	Maclean (1971)
KNP	late	heavy rain on 19 March	displaying on 26 March	Johnson (1983)
N Cape	late	heavy rain 18–23 May	eggs & chicks at end of May	Winterbottom and Rowan (1962)
Karoo	late	Feb/Mar rain	eggs & chicks in May	Martin and Martin (1970)
Chestnut Weaver				
Namibia	late	Dec–Feb rains	eggs laid in large colonies	Braine and Braine (1971)
Cape Weaver				
W Cape	early	very wet April	breeding started 4 weeks early: nests in June; eggs in July	Rowan (1953)
Karoo	late	Feb/Mar rain	building in May	Martin and Martin (1970)
Lesser Masked Weaver				
Botswana	late	good, late rains	nests built in vast colonies	Cole (1958)
Southern Red Bishop				
Karoo	late	heavy rain Jan–March	chicks in April	Martin *et al.* (1985, 1986)
former Transvaal	late	long, severe winter	nest building in November, rather than in October	Haagner (1901)
Red-collared Widow				
Mozambique	prolonged	prolonged good rains	breeding continued during dry season	Brooke (1966b)
White-winged Widow				
KNP	late	heavy rain on 19 March	mating & displaying on 23 March	Johnson (1983)

Table 3: Clutch sizes, incubation and fledging periods, and sizes of weavers in southern Africa (data from Fry and Keith 2004)

Species	Mean clutch size	Incubation period (days)	Fledging period (days)	Incubation + Fledging (days)	Mass of female (g)	Wing of female (mm)	Tarsus of female (mm)
Red-billed Buffalo-weaver *Bubalornis niger*	3.5	11	21.5	32.5	81.3	115.0	29.5
White-browed Sparrow-weaver *Plocepasser mahali*	2	15	20	35	46.3	101.5	26.2
Sociable Weaver *Philetairus socius*	3.5	13.5	22	35.5	27.3	70.7	17.0
Scaly-feathered Finch *Sporopipes squamifrons*	4	11	16	27	12.4	56.0	15.0
Thick-billed Weaver *Amblyospiza albifrons*	3	15	20.5	35.5	40.0	85.8	22.0
Dark-backed Weaver *Ploceus bicolor*	3	16	22	38	32.0	83.5	27.0
Olive-headed Weaver *Ploceus olivaceiceps*	2.5	–	–	–	19.6	77.8	18.5
Spectacled Weaver *Ploceus ocularis*	3	13.5	17	30.5	28.2	73.3	24.5
Village Weaver *Ploceus cucullatus*	2.5	12.2	19	31.2	38.1	81.4	20.5
Chestnut Weaver *Ploceus rubiginosus*	3.5	12.5	14.5	27	28.0	79.0	22.0
Cape Weaver *Ploceus capensis*	2.5	13.5	17	30.5	40.4	84.5	22.5
Southern Masked Weaver *Ploceus velatus*	2.5	13	16.5	29.5	25.7	80.3	21.0
Lesser Masked Weaver *Ploceus intermedius*	2.5	12.5	15.5	28	21.9	69.0	20.0
Golden Weaver *Ploceus xanthops*	2	14	20.5	34.5	39.0	83.6	24.0
Yellow Weaver *Ploceus subaureus*	2.5	–	20.5	–	26.4	77.1	21.1
Southern Brown-throated Weaver *Ploceus xanthopterus*	2.5	15.5	16.5	32	19.1	64.6	20.0
Red-headed Weaver *Anaplectes melanotis*	2.5	12	17	29	22.0	77.6	19.0
Red-billed Quelea *Quelea quelea*	3	11	10.5	21.5	19.0	65.0	18.0
Red-headed Quelea *Quelea erythrops*	2	13	13	26	21.1	60.0	17.0
Southern Red Bishop *Euplectes orix*	3	12.5	13	25.5	20.7	66.3	21.5
Black-winged Bishop *Euplectes hordeaceus*	3	12.5	12	24.5	19.0	66.5	20.0
Yellow-crowned Bishop *Euplectes afer*	3.5	13	17	30	15.3	61.8	17.3
Yellow Bishop *Euplectes capensis*	3	14.5	18	32.5	30.4	71.6	23.0
Fan-tailed Widow *Euplectes axillaries*	3	12.5	15.5	28	22.0	71.1	23.5
White-winged Widow *Euplectes albonotatus*	3	13	12.5	25.5	18.9	66.2	18.0
Yellow-mantled Widow *Euplectes macrourus*	2.5	13	15	28	19.7	68.3	19.5
Red-collared Widow *Euplectes ardens*	3	13.5	15.5	29	19.1	66.8	20.5
Long-tailed Widow *Euplectes progne*	3	13	17	30	32.0	93.0	23.3

Table 4: Estimates of the primary moult parameters of southern African weavers using the maximum likelihood method of Underhill and Zucchini (1987); this summary contains the results for all species analysed in this thesis (except those of Chapter 8), and also results from * Oschadleus *et al.* (2000) and # Craig *et al.* (2001)

Species	Group (Locality, race, years)	Mean start date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Standard error (days)	Mean end date	Standard error (days)	n
Sociable Weaver	*eremnus* (SA)	31 Dec	6.1	38.0	2.2	168.9	8.1	17 Jun	3.7	481
	geminus	28 Jan	5.9	67.5	5.0	215.8	13.8	31 Aug	12.0	231
	socius	26 Jan	4.1	37.7	1.9	151.7	7.2	26 Jun	3.8	838
Spectacled Weaver	KwaZulu-Natal	3 Feb	3.4	21	1.3	114.1	4.3	28 May	2.3	388
Cape Weaver	Western Cape, 1998–2003, grid 3318	11 Nov	1.4	24.2	0.6	98.1	2.0	17 Feb	1.3	3226
	KwaZulu-Natal, 1998–2003, grid 2930	2 Feb	4.1	31.5	2.7	124.2	9.5	6 Jun	7.4	238
	Eastern Cape #	9 Jan	4	25.2	2.1	106	7	25 Apr	4.7	316
Yellow Weaver	KwaZulu-Natal	27 Feb	2.6	19.7	1.4	65.8	3.9	4 May	2.8	653
Southern Masked Weaver	Western Cape, 1986–1995 *	9 Jan	7.5	24.0	2.1	73.8	13.2	24 Mar	6.5	2318
	Western Cape, 1998–2003, grid 3318	27 Dec	2.4	33.2	1.2	84.4	3.3	22 Mar	2.2	1411
	North-west Province, 1983–1995 *	15 Feb	2.7	22.7	1.6	80.4	3.9	7 May	2.5	1547
	Gauteng, 1998–2003	11 Feb	0.9	18.8	0.6	75.9	1.7	28 Apr	1.3	2556
	Eastern Cape #	22 Mar	3	24.8	1.9	67	5	28 May	3.6	391
Village Weaver	KwaZulu-Natal, grid 2930	12 Feb	2.4	28.5	1.1	96.1	3.4	19 May	2.1	1215
	Eastern Cape #	17 Feb	5	40.1	2.4	109	6	5 Jun	3.7	436
Chestnut Weaver	male	9 Apr	2.9	39.5	1.2	205.8	3.8	1 Nov	1.8	975
	female	30 Apr	3.2	37.5	1.5	189.4	4.8	5 Nov	2.9	552
Red-billed Quelea	Namibia, 1999–2004	21 May	4.3	37.4	1.9	74.6	4.8	3 Aug	2.7	1163
	Botswana, 1999–2004	31 May	3.6	35.1	1.8	82.5	4.5	21 Aug	2.6	543
	Gauteng, 1999–2004	23 Apr	2.6	32.7	1.2	100.9	3.6	2 Aug	2.4	1105
	Eastern Cape #	6 Apr	2	36.5	0.8	124	3	8 Aug	1.4	3077
Southern Red Bishop	Western Cape, 1998–2003, grid 3318	13 Dec	1.1	25.3	0.6	88.6	1.7	12 Mar	1.2	3154
	Gauteng, 1998–2003	23 Mar	1.5	35.1	1.1	71.9	2.5	3 Jun	2.3	4808
	Eastern Cape #	28 Apr	4	47.3	2.9	89	7	26 Jul	6.1	622
Yellow Bishop	Western Cape, grids 3318 & 3418	4 Dec	2.0	23.3	1.0	103.4	3.0	17 Mar	1.8	777
Fan-tailed Widow	KwaZulu-Natal, grid 2930	2 Apr	1.9	18.1	0.9	50.5	2.8	23 May	2	1002

Table 4 continued

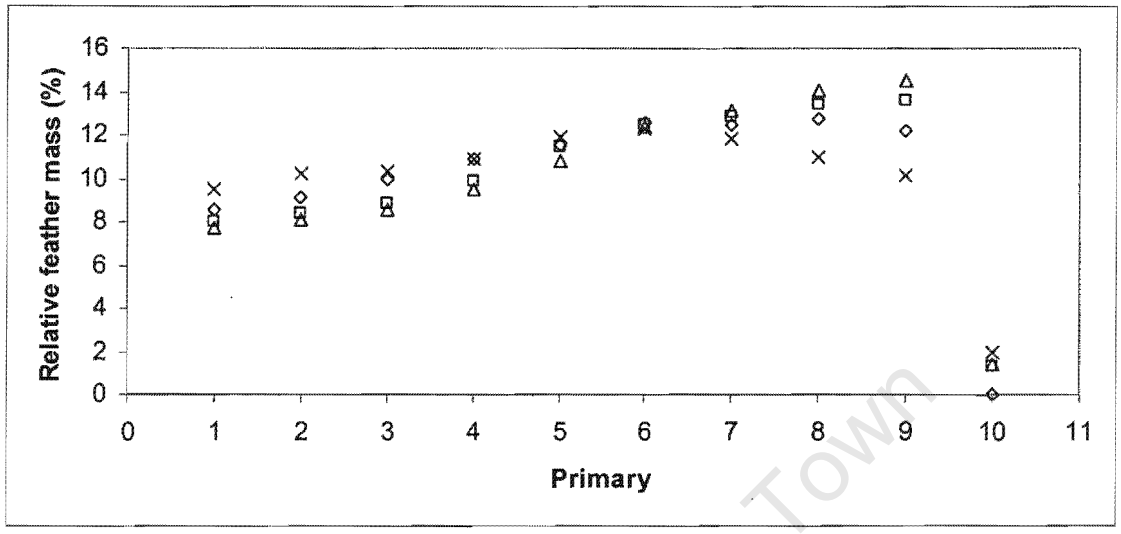
Species	Group (Locality, race, years)	Mean start date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Standard error (days)	Mean end date	Standard error (days)	n
White-winged Widow	Gauteng	18 Apr	2.5	26.3	1.6	46.5	3.3	3 Jun	2.6	685
Red-collared Widow	Gauteng	5 Apr	2.5	30.8	1.6	59.9	3.5	3 Jun	2.6	667
Long-tailed Widow	Eastern South Africa	26 Mar	4.8	20.6	2.9	60.7	8.7	25 May	7.1	279
Thick-billed Weaver	Gauteng	20 Feb	4.3	23.8	2.6	71.2	6.8	2 May	5.4	179
	KwaZulu-Natal	26 Mar	3.9	22.9	2.2	73.3	6.4	8 Jun	5.2	462

Table 5: Growth rates of individual primary feathers in southern African weavers
Localities are abbreviations for countries or for South African provinces: NA=Namibia, BW=Botswana, WC=Western Cape, EC=Eastern Cape, NC=Northern Cape, KZN=KwaZulu-Natal, FS=Free State, GP=Gauteng

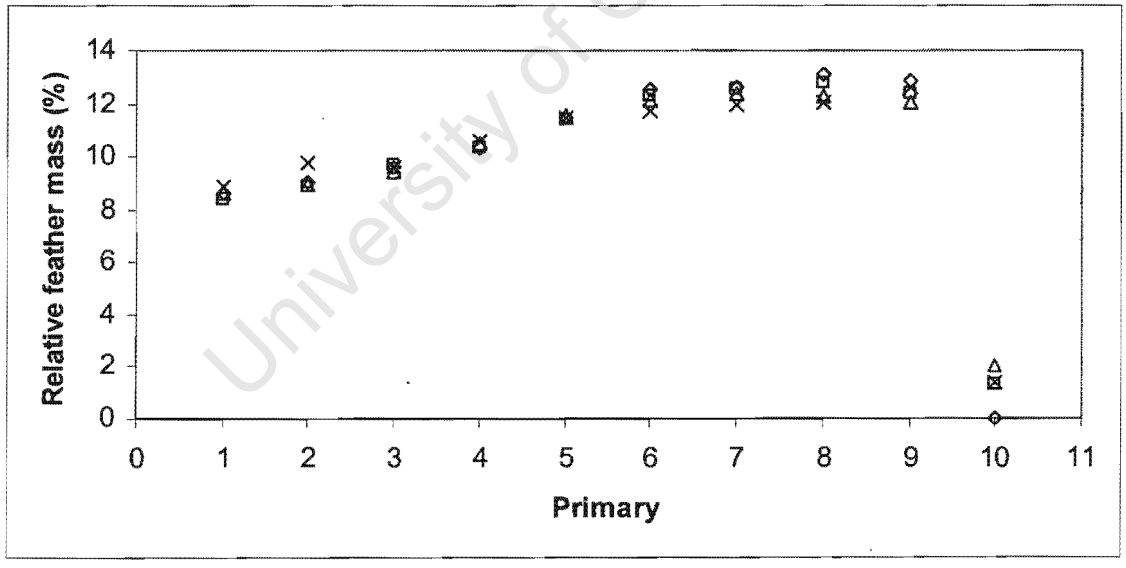
		Growing primaries		Individual mean	Wing-moult
Species	Area	Range	Mean	rate (days)	duration (days)
Sociable Weaver	NA+NC	1–4	1.2	24.1	
Spectacled Weaver	KZN	1–4	1.7		114.1
Cape Weaver	KZN	1–4	1.9		124.2
Cape Weaver	WC	1–4	1.9		98.1
Yellow Weaver	KZN	1–3	1.7		65.8
Southern Masked Weaver	GP	1–4	1.9		75.9
Southern Masked Weaver	WC	1–4	1.9		84.4
Village Weaver	KZN	1–4	1.6		96.1
Chestnut Weaver	NA	1–2	1.1	15.3	205.8
Red-billed Quelea	NA	1–2	1.0	9.8	74.6
Red-billed Quelea	BW	1–3	1.1	14.0	82.5
Red-billed Quelea	GP	1–4	1.7	28.4	100.9
Red-billed Quelea	EC	1–4	1.7	23.9	124
Red Bishop	GP	1–5	1.7		71.9
Red Bishop	WC	1–4	1.7		88.6
Cape Bishop	WC	1–4	1.8	21.3	103.4
Fan-tailed Widow	KZN	1–3	1.9	11.3	50.5
White-winged Widow	GP	1–4	1.7	8.0	46.5
Red-collared Widow	GP	1–5	2.1	14.4	59.9
Long-tailed Widow	all	1–4	2.3		60.7
Thick-billed Weaver	KZN	1–3	1.8		73.3
Thick-billed Weaver	GP	1–3	1.9		71.2

Figure 1: Relative primary masses for southern African weavers

(a) Sociable Weaver, diamonds; Chestnut Weaver female, squares; Chestnut Weaver male, triangles, Thick-billed Weaver, crosses



(b) Village Weaver, diamonds; Cape Weaver, squares; Southern Masked Weaver, triangles; Lesser Masked Weaver, crosses



(c) Red-billed Quelea, diamonds; Red Bishop, squares; White-winged Widow, triangles; Long-tailed Widow, crosses

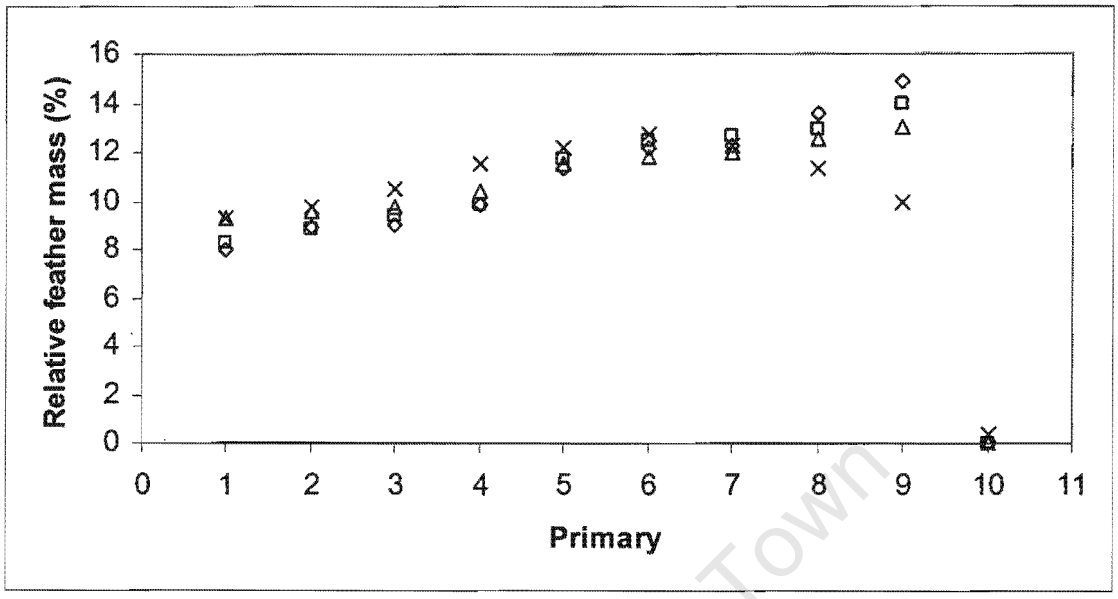


Figure 2: Plot of S against –T for southern African weavers
1=Sociable Weaver, 2=Thick-billed Weaver, 3=Chestnut Weaver male, 4=Chestnut Weaver female, 5=Village Weaver, 6=Cape Weaver, 7=Southern Masked Weaver, 8=Lesser Masked Weaver, 9=Red-billed Quelea, 10=Red Bishop, 11=White-winged Widow, 12=Long-tailed Widow

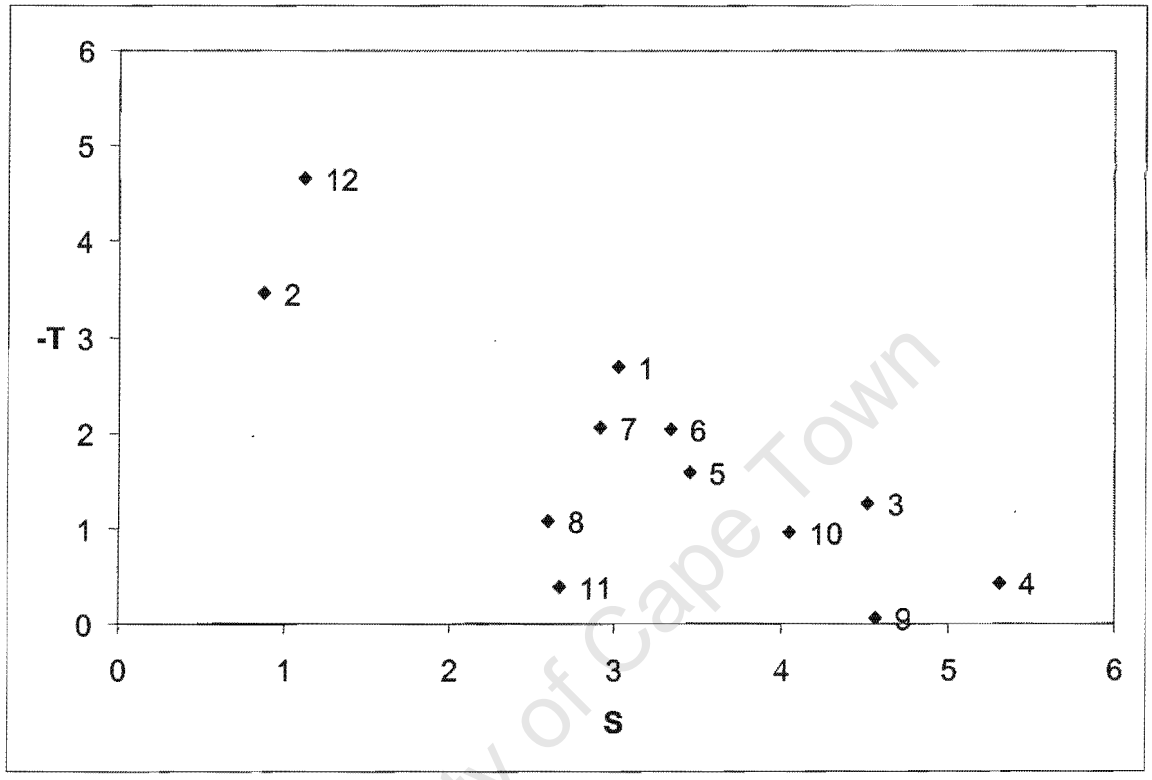


Figure 3: Median months of egg-laying for southern African weavers (from Prŷs-Jones and Newton unpublished data, Zimbabwe data from Irwin 1981). For Thick-billed Weaver in the former Transvaal my own records from Gauteng have been added. For Southern Masked Weavers additional breeding records from northern KwaZulu-Natal are included. For each region the median month of egg-laying per species is shown; symbols indicate genus: open squares are *Ploceus* species, open diamonds are *Euplectes* species, crosses are other species (data in Appendix 1); species with <10 records in an area are omitted

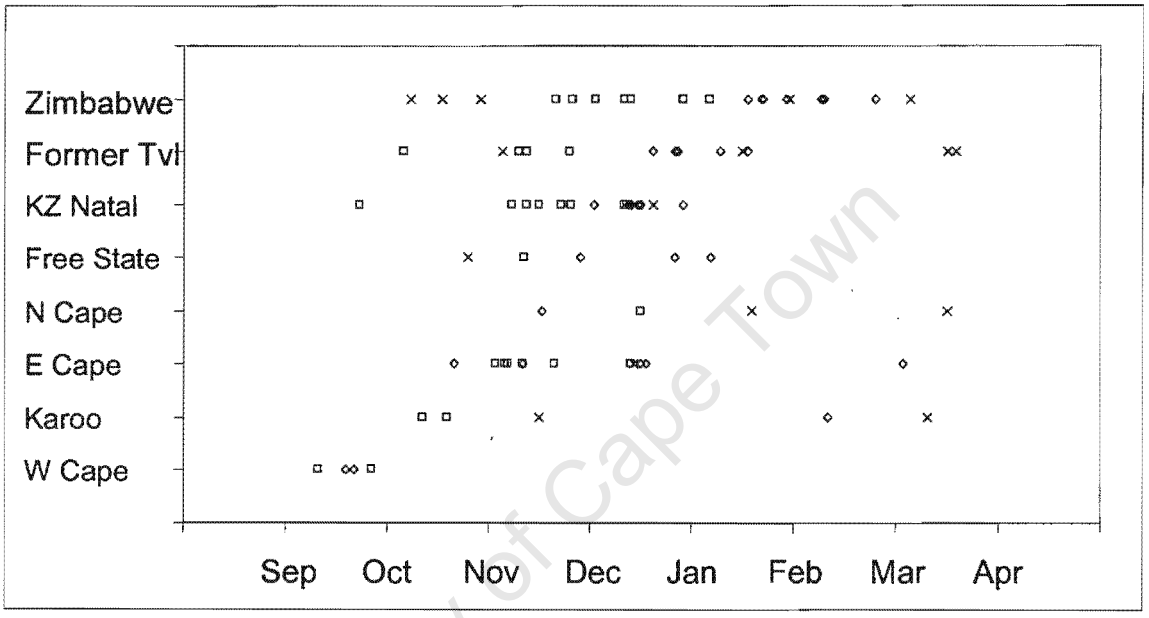
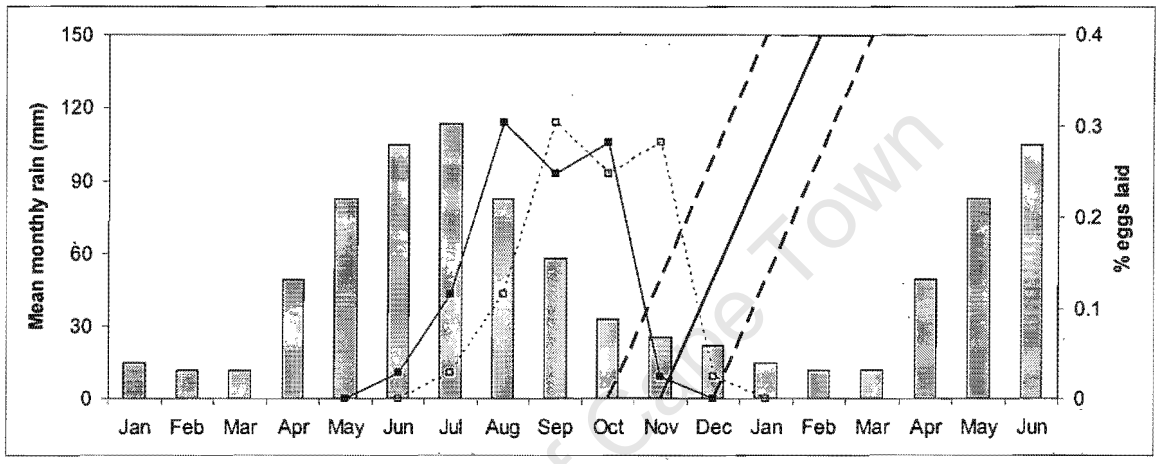


Figure 4: Diagrammatic representation of the annual cycle of southern African weavers. Grey bars show mean monthly rainfall; the solid line joining solid squares shows the percentage of eggs laid per month (from the Nest Record Cards summary by Prŷs-Jones and Newton unpublished data); the dotted line joining open squares shows when the breeding cycle finishes (egg laying date plus incubation plus fledging periods); the solid diagonal line joins the estimated mean start and end dates of moult, while the diagonal dotted lines show the approximate 95% confidence intervals of moult scores on any given date

(a) Cape Weaver annual cycle in a winter rainfall region (rainfall is mean monthly rainfall for 1993–2003 at Altydgedacht rainfall station)



(b) Cape Weaver annual cycle in a summer rainfall region (mean monthly rainfall for Johannesburg, Gauteng)

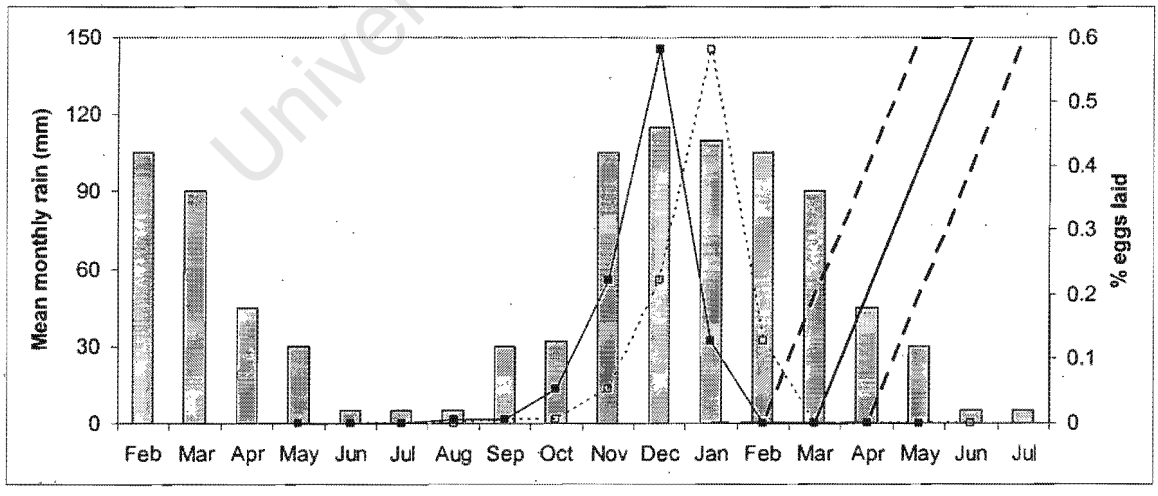
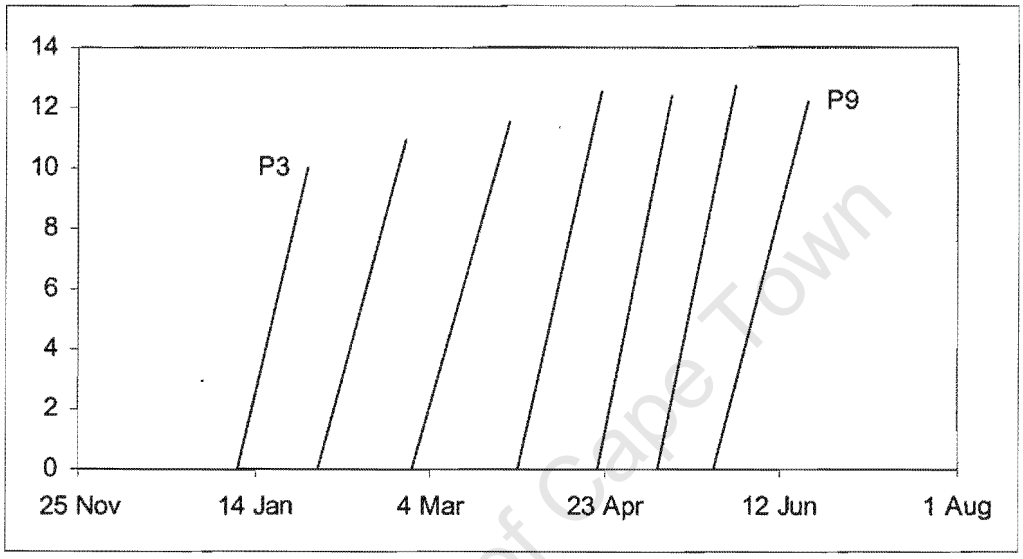
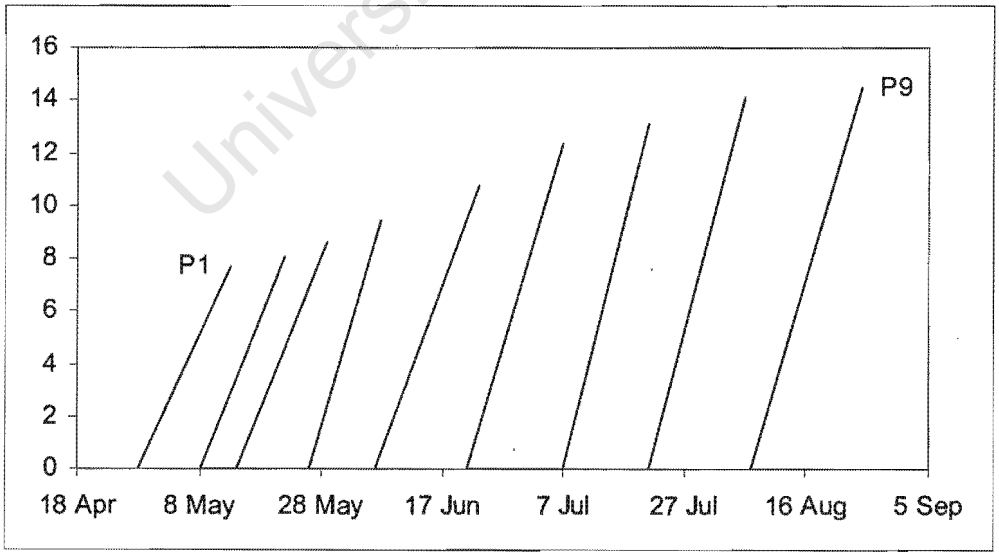


Figure 5: Timing of moult of each of the nine primaries of southern African weavers. The x–axis represents the date; the y–axis the percentage primary mass (from Table 1). Each line represents one primary (1 to 9 from left to right, in some species less than 9 primaries – see Tables in chapters). For each line, the starting date is shown on the x–axis; the height to which the line rises shows the percentage primary mass; the end-point of the line is directly above the completion date on the x–axis. Thus the slope of the line gives the rate at which feather material is deposited; steep slopes represent rapid growth

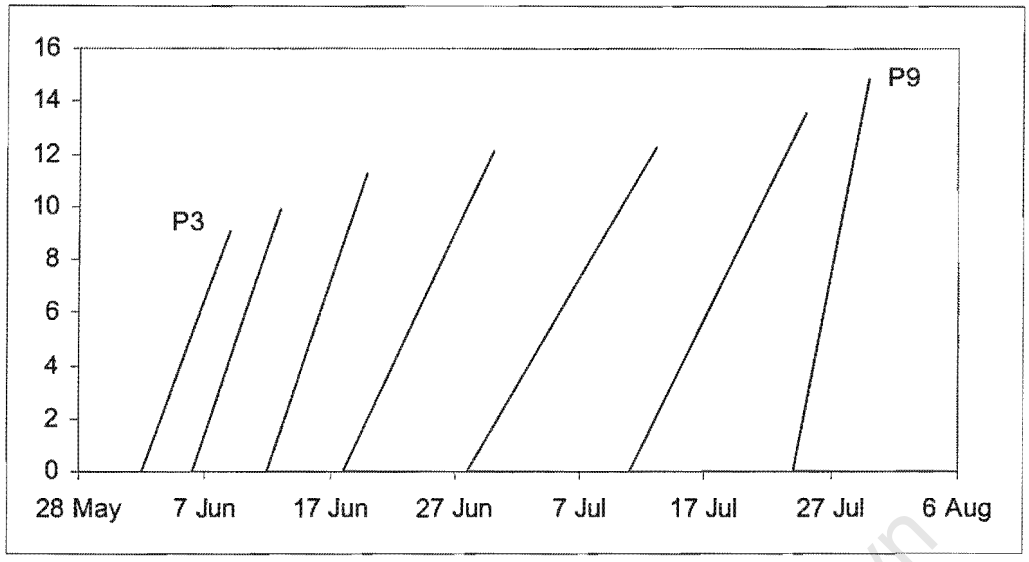
(a) Timing and rate of individual primary feather growth in Sociable Weavers in the Northern Cape



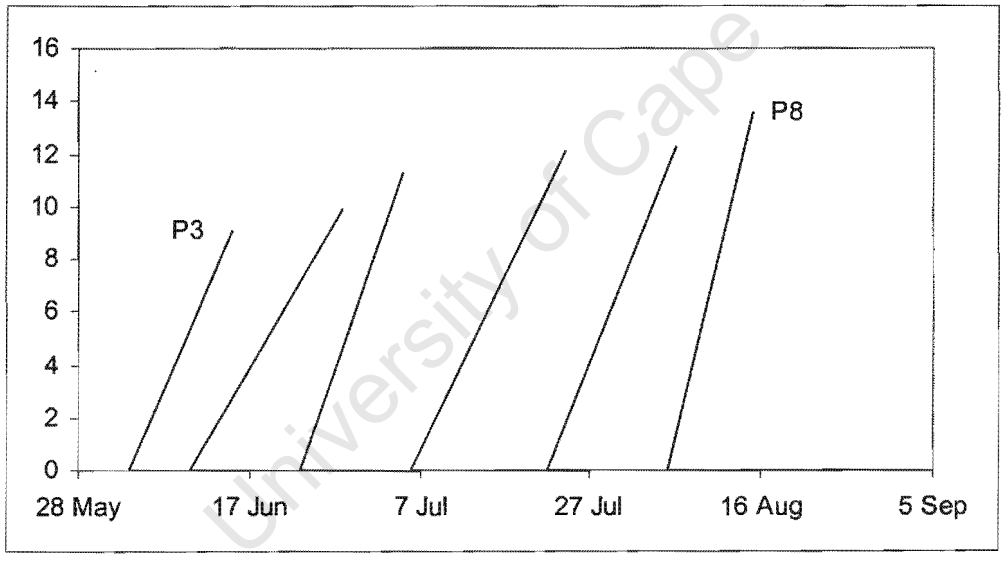
(b) Timing and rate of individual primary feather growth in Chestnut Weaver males in Namibia



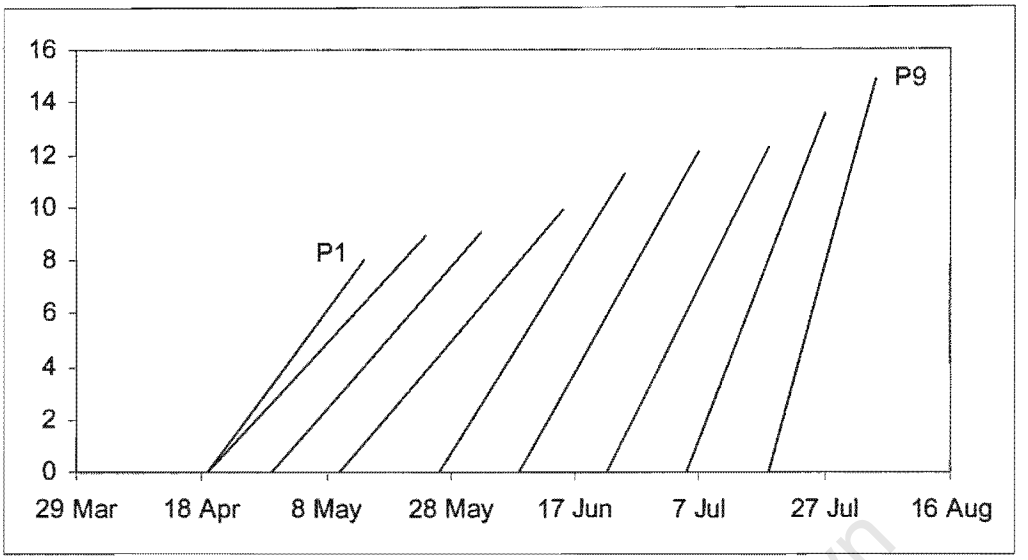
(c) Timing and rate of individual primary feather growth in Red-billed Quelea in Namibia



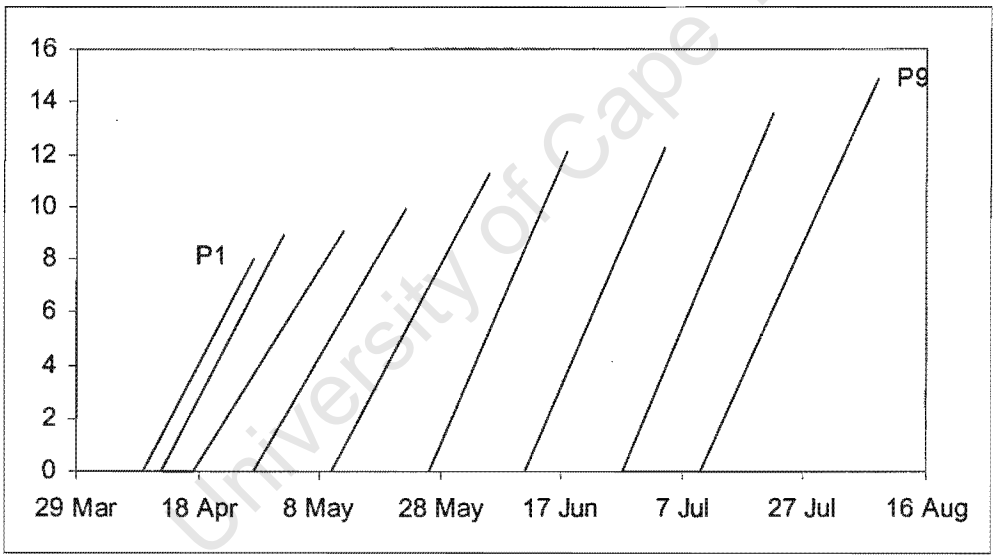
(d) Timing and rate of individual primary feather growth in Red-billed Quelea in Botswana



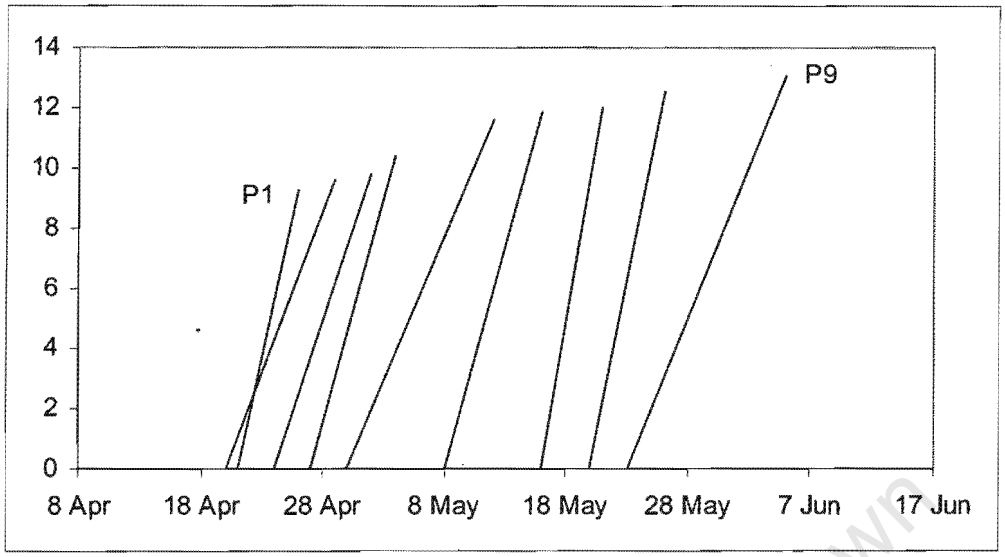
(e) Timing and rate of individual primary feather growth in Red-billed Quelea in Gauteng



(f) Timing and rate of individual primary feather growth in Red-billed Quelea in the Eastern Cape



(g) Timing and rate of individual primary feather growth in White-winged Widows in Gauteng



Appendix 1

Months of egg-laying for southern African weavers

Appendix 1: Months of egg-laying (percentages) for southern African weavers (from Prŷs-Jones and Newton unpublished data, Zimbabwe data from Irwin 1981). For Thick-billed Weaver in the former Transvaal my own records from Gauteng have been added. For Southern Masked Weavers additional breeding records from northern KwaZulu-Natal are included. The percentages are summarized as 5th percentile (represents start of moult), 95th percentiles (end of moult), range (90% range of months of egg-laying) and median egg-laying month; numbers represent parts of months, e.g. 12.5 = mid December, 12.4 = 40% through December
Here the data are presented by region, then by species
Calculations of the 5th and 95th percentiles, the range, and the median are excluded where sample size<10

Area	Species	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	n	5th	95th	Range	Median
Western Cape																		
	Cape Weaver	12	30	25	28	3							3	1225	7.4	11.1	3.7	9.3
	Yellow Bishop	0	23	44	26	5	1							239	8.2	11.2	3.0	9.6
	Southern Red Bishop	0	18	47	25	10	0							1109	8.3	11.5	3.3	9.7
	Southern Masked Weaver	1	15	40	14	20	9	1						205	8.3	12.5	4.3	9.8
Karoo																		
	Cape Weaver			38	35	27								48	9.1	11.8	2.7	10.4
	Southern Masked Weaver	1	9	14	42	16	11	2			1	2		85	8.4	1.4	5.0	10.6
	Scaly-feathered Finch	5	9	14	18	9			5	5	14	18	5	22	8.1	6.0	9.9	11.5
	Sociable Weaver	33											67	3				
	Yellow Bishop		25	50		25								4				
	Yellow-crowned Bishop								100					7				
	Southern Red Bishop		2	6	34	4		1	6	43	3			96	9.5	4.0	6.5	2.3
	Red-billed Quelea					28				73				40	11.2	3.9	4.7	3.3
Northern Cape																		
	Southern Red Bishop				5	86	9							22	11.0	12.5	1.4	11.5
	White-browed Sparrow-weaver			22	33		22		11			11		9				
	Southern Masked Weaver					34	31	13		22				32	11.1	3.8	4.6	12.5
	Sociable Weaver	7	5	7	7	5	12	9	6	1	13	15	11	605	7.7	6.6	10.9	1.6
	Scaly-feathered Finch	9		2	2			7	18	24	9	18	11	45	7.6	6.6	11.0	3.5
Eastern Cape																		
	Long-tailed Widow			20	45	25		10						20	9.3	1.5	4.3	10.7

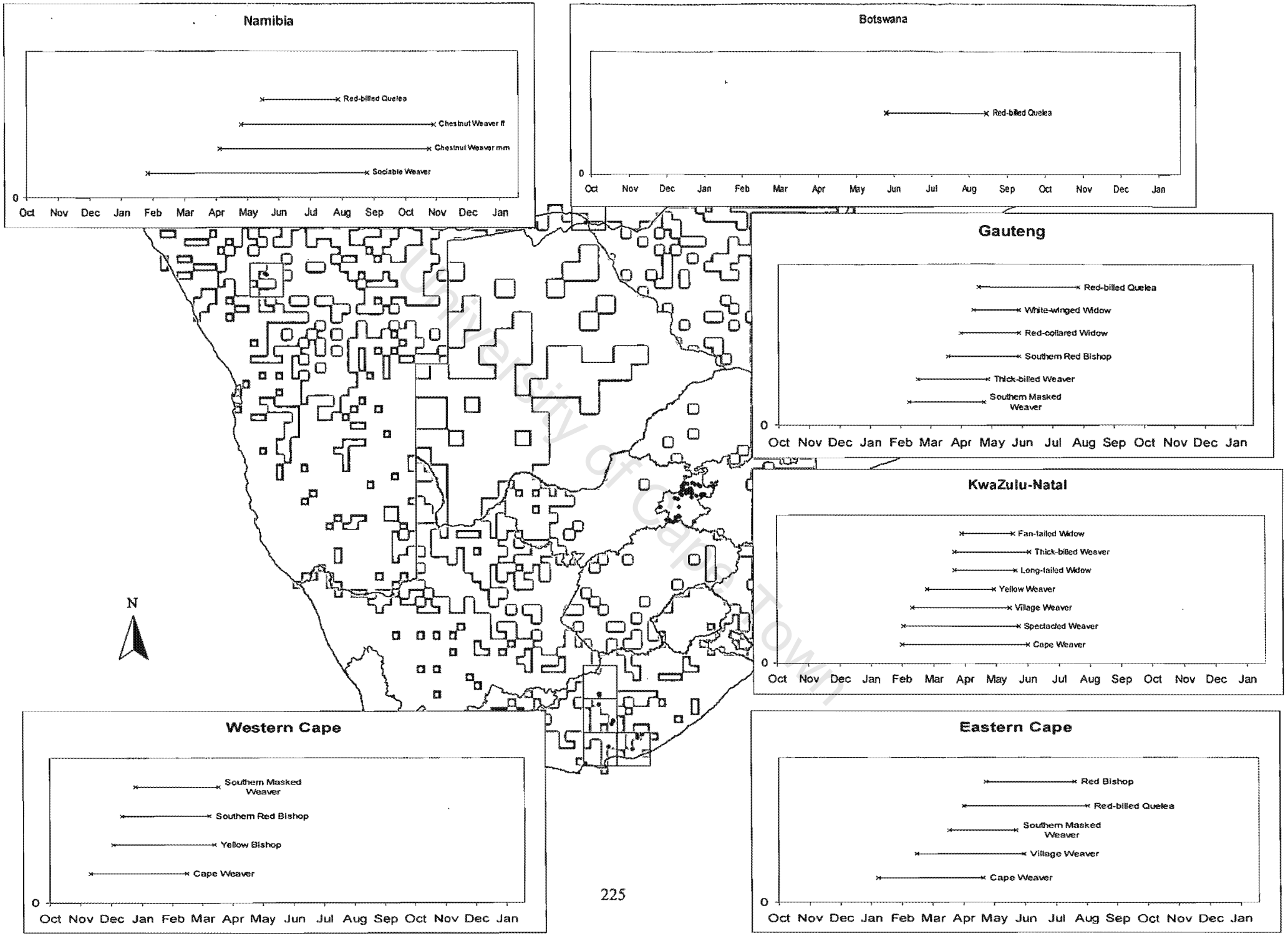
Area	Species	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	n	5th	95th	Range	Median
Eastern Cape continued																		
	Southern Masked Weaver		2	23	23	32	16	5						44	9.1	13.0	3.9	11.1
	Yellow Weaver			17	29	25	4	25						24	9.3	1.8	4.5	11.2
	Cape Weaver	5	4	13	21	35	15	2		1	1		2	97	8.0	1.6	5.6	11.2
	Red-collared Widow			14	25	32	7	4	18					28	9.4	2.7	5.4	11.3
	Spectacled Weaver			6	32	35	21	6						34	9.9	1.2	3.3	11.3
	Dark-backed Weaver			5	11	53	26	5						19	10.0	1.1	3.1	11.7
	Village Weaver				20	10	50	20						10	10.3	1.8	3.5	12.4
	Thick-billed Weaver			5	5	14	64	9	5					22	10.1	2.0	3.9	12.4
	Yellow Bishop			9	18		45	18	9					11	9.6	2.5	4.9	12.5
	Fan-tailed Widow					25	50		25					16	11.2	2.8	3.6	12.5
	Southern Red Bishop			1	3	15	58	14	8	2				160	11.1	2.6	3.5	12.6
	Yellow-crowned Bishop						13	27	7	47	7			15	12.4	4.3	3.9	3.1
Free State																		
	White-browed Sparrow-weaver		7	25	23	30	16							44	8.7	12.7	4.0	10.8
	Southern Masked Weaver			9	29	34	12	15	1					82	9.6	1.7	4.2	11.4
	Long-tailed Widow				9	45	26	6	13	1				152	10.5	2.7	4.2	11.9
	Yellow Bishop						100							1				
	Red-billed Quelea								100					1				
	Sociable Weaver						50					50		2				
	Red-collared Widow							100						3				
	Cape Weaver				25		50	25						4				
	Scaly-feathered Finch			50						50				4				
	Yellow-crowned Bishop					6	53	12	24	6				17	11.9	3.2	3.3	12.8
	Southern Red Bishop					3	36	56	4	0	0			240	12.1	2.0	1.9	1.2
KwaZulu-Natal																		
	Southern Masked Weaver			15	2	3	55	25						89	9.3	1.8	4.5	12.5
	Yellow Weaver			18	23	38	13	7	0					267	9.3	1.4	4.1	11.2
	Southern Brown-throated Weaver				29	57	14							14	10.2	12.7	2.5	11.4
	Dark-backed Weaver				38	23	23	15						13	10.1	1.7	3.5	11.5
	Spectacled Weaver			9	18	32	34	7						56	9.6	1.3	3.7	11.7

Area	Species	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	n	5th	95th	Range	Median
KwaZulu-Natal continued																		
	Village Weaver			15	3	39	34	9						98	9.3	1.5	4.1	11.8
	White-browed Sparrow-weaver							100						1				
	Golden Weaver					25	25	50						4				
	Yellow-crowned Bishop						13	88						8				
	Red-collared Widow				17	31	36	13	2	2				64	10.3	1.9	3.6	12.0
	Lesser Masked Weaver				31	8	35	19	8					26	10.2	2.4	4.2	12.3
	Cape Weaver		1	1	5	22	58	13						148	10.7	1.6	2.9	12.4
	Long-tailed Widow			3		38	25	22	13					32	11.1	2.6	3.6	12.4
	Fan-tailed Widow			4	5	24	40	18	7	1				148	10.2	2.5	4.3	12.4
	Southern Red Bishop				6	12	67	13	1	1				1276	10.8	1.8	2.9	12.5
	Yellow Bishop					10	80	10						10	11.5	1.5	2.0	12.5
	Thick-billed Weaver		1	2	10	13	39	23	13					101	10.2	2.6	4.4	12.6
	White-winged Widow					13	41	38	6		3			32	11.4	2.7	3.3	12.9
Former Transvaal (includes Gauteng)																		
	Village Weaver		7	40	16	24	9	2	2					55	8.7	12.9	4.2	10.2
	White-browed Sparrow-weaver	4	8	16	20	22	14	6	6			4	2	51	8.1	5.2	9.1	11.1
	Cape Weaver		8	14	22	23	25	9						65	8.7	1.5	4.8	11.3
	Southern Masked Weaver	0	6	14	20	27	18	10	5	0		0		512	8.8	2.1	5.3	11.4
	Lesser Masked Weaver			7	14	36	14	21	7					14	9.7	2.3	4.6	11.8
	Thick-billed Weaver		10	20	10	20	20	20						10	9.5	1.8	4.3	11.5
	Golden Weaver							100						3				
	Spectacled Weaver				20	40	40							5				
	Red-headed Weaver			33	17	17	17	17						6				
	Sociable Weaver					43	29			29				7				
	Yellow Bishop					14	29	14	43					7				
	Fan-tailed Widow				11	67	11	11						9				
	Red-collared Widow				4	18	46	25	4	4				28	11.1	2.6	3.5	12.6
	Southern Red Bishop				2	20	34	30	10	4				1043	11.2	2.9	3.8	12.8
	Long-tailed Widow				7	17	30	31	13	2				87	10.7	2.8	4.1	12.9
	White-winged Widow				1	4	37	26	29	3				70	11.8	2.9	3.1	1.3

Area	Species	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	n	5th	95th	Range	Median
Former Transvaal (includes Gauteng) continued																		
	Red-billed Buffalo-weaver				6	22	11	22		39				18	10.9	3.9	5.0	1.5
	Yellow-crowned Bishop					1	19	54	13	11	2			104	12.2	3.7	3.5	1.6
	Red-billed Quelea						18		6	53	6	18		17	12.3	5.7	5.4	3.5
	Scaly-feathered Finch	4	3	2	3	2	4	15	12	6	25	17	5	207	8.2	6.0	9.8	3.6
Zimbabwe																		
	Red-billed Quelea	3	3	35	41	16	3							37	8.9	11.9	3.0	10.2
	Red-headed Weaver	0	7	21	40	21	5	4	0					205	8.7	13.0	4.3	10.5
	White-browed Sparrow-weaver		1	14	38	19	7	9	9	3	1			117	9.3	2.9	5.6	10.9
	Dark-backed Weaver			21		43	21	7	7					14	9.2	2.3	5.1	11.7
	Lesser Masked Weaver		0	6	21	27	17	21	6	2				219	9.7	2.5	4.8	11.8
	Southern Brown-throated Weaver					25		75						4				
	Southern Masked Weaver	0	4	11	18	17	11	19	12	9	0			1009	9.1	3.5	6.4	12.1
	Golden Weaver		0	9	20	14	17	21	14	3	0			298	9.5	2.9	5.4	12.3
	Spectacled Weaver			5	13	18	34	13	14	3				104	10.0	2.9	4.8	12.4
	Thick-billed Weaver					19	34	31	8	9				129	11.3	3.4	4.1	12.9
	Village Weaver		1	16	16	7	7	16	29	6	1			614	9.3	3.4	6.1	1.2
	Southern Red Bishop					0	22	50	19	8	0			3029	12.2	3.4	3.2	1.5
	Red-collared Widow						14	53	21	11	2			259	12.4	3.7	3.3	1.7
	Yellow-mantled Widow						19	45	22	14				85	12.3	3.6	3.4	1.7
	Yellow Bishop						15	37	34	12	2			458	12.3	3.7	3.4	1.9
	Red-billed Buffalo-weaver			5	2	7	12	26	30	16	2			43	10.2	3.8	5.7	2.0
	White-winged Widow						7	35	29	22	7			263	12.7	4.3	3.6	2.3
	Yellow-crowned Bishop						5	35	35	26				43	1.0	3.8	2.8	2.3
	Black-winged Bishop							11	49	35	5			57	1.5	4.1	2.6	2.8
	Scaly-feathered Finch	3	2	7	8	2	3	8	11	49	5	3		330	9.1	4.5	7.5	3.1

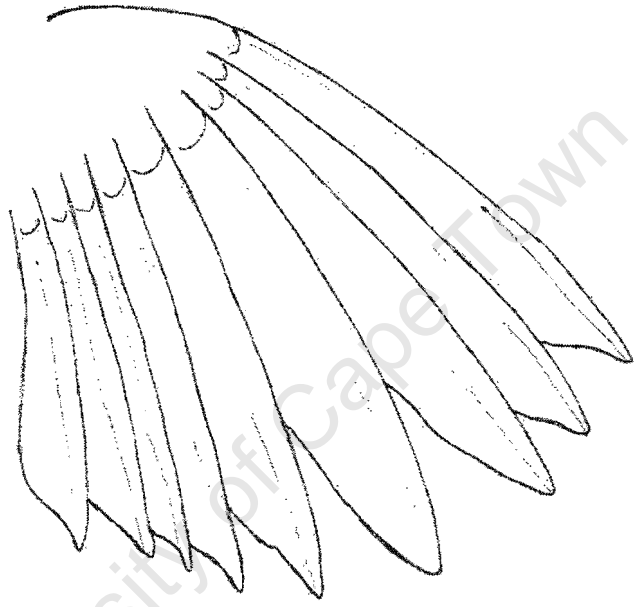
Appendix 2

Timing and duration of primary moult in southern African weavers



Appendix 3

Plates illustrating breeding and moult in African weavers



Appendix 3: Plates illustrating breeding and moult in African weavers

Plate 1: Breeding

1. Sociable Weaver nest in *Acacia erioloba* tree (Wiese farm, near Windhoek, Namibia, May 2004)
2. Thick-billed Weaver male building nest (National Botanic Gardens, Pretoria, South Africa, January 2004)
3. Southern Masked Weaver colony on barbed wire fence (near Wakkerstroom, Mpumulanga, South Africa, January 2004) an adaptation allowing it to expand its breeding range into grassland areas
4. Village Weaver multi-male colony (near Dundee, KwaZulu-Natal, South Africa, December 2002)
5. Golden Palm Weaver *Ploceus bojeri* male displaying from incomplete nest (Turtle Bay, Kenya, September 2004)
6. Southern Red Bishop nest in grass; their nests are usually in reed-beds

Plate 2: Moult

1. Sociable Weaver – the first seven primaries are new, the eighth primary has started growing, the ninth (and vestigial tenth) are old feathers (Wiese farm, near Windhoek, Namibia, May 2004)
2. Southern Masked Weaver male showing the first three primaries growing simultaneously; body moult is in progress (Rondevlei Bird Sanctuary, Western Cape, November 2001)
3. Southern Red Bishop male and female – many weavers show extreme sexual and seasonal dimorphism, with males sporting bright colours in the breeding season, and resembling the duller females in the non-breeding season (Lamberts Bay, Western Cape, October 2001)
4. Cape Weaver male with completed moult (Robben Island, Western Cape, October 2004)
5. Red-billed Quelea male completing prenuptial body moult – some pins of growing feathers are still visible on the head (Wakkerstroom, Mpumulanga, South Africa, December 2002)
6. Fan-tailed Widow male, showing russet underwing coverts, a feature present in both sexes all year round, allowing this species to be identified in the hand from other similar *Euplectes* species (Wakkerstroom, Mpumulanga, South Africa, January 2004)

Plate 1: Breeding in weavers. Left to right, top to bottom: Sociable Weaver, Thick-billed Weaver, Southern Masked Weaver, Village Weaver, Golden Palm Weaver, Southern Red Bishop

Plate 2: Moult in weavers. Left to right, top to bottom: Sociable Weaver, Southern Masked Weaver, Southern Red Bishop, Cape Weaver, Red-billed Quelea, Fan-tailed Widow